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Patterns of Post-Fire Aspen Seedling Establishment, Growth, and Mortality in the Western United States

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PATTERNS OF POST-FIRE ASPEN SEEDLING ESTABLISHMENT, GROWTH, AND MORTALITY IN THE WESTERN UNITED STATES

by

Mark Regier Kreider

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

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ABSTRACT

Patterns of Aspen Seedling Establishment, Growth, and Mortality

in the Western United States

by

Mark Regier Kreider, Master of Science

Utah State University, 2021

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Department: Wildland Resources

Sexual seedling establishment in aspen is increasingly recognized as an important natural regeneration pathway for the species in the western U.S. However, information on seedling abundance as well as factors influencing aspen sexual regeneration is limited and frequently anecdotal, due to historical assumptions of seedling rarity as well as difficulty identifying sexual seedlings from asexual aspen sucker regeneration. This thesis contributes to the field of aspen seedling ecology in three major ways. Chapter 1 utilizes historical aspen seedling occurrences in the western U.S. and a systematic field survey of 2018 fire footprints to explore patterns and test assumptions of aspen seedling establishment across multiple geographic scales. Chapter 2 focuses on one widespread post-fire aspen seedling establishment event in southern Utah, tracking seedlings through time to identify factors that influence survival and growth across a range of environmental conditions. Finally, Chapter 3 is reproduced from a first-authored article published in the Journal of Forestry and presents a framework for non-destructively

distinguishing aspen seedlings from suckers, removing a barrier that has hampered aspen seedling research in the past. Together, these chapters expand our understanding of aspen seedling establishment in the western U.S., and highlight the important role sexual aspen establishment may play in the dispersal and recruitment of the species, both historically and in changing future conditions.

(124 pages)

PUBLIC ABSTRACT

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Mark Regier Kreider

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PREFACE

Because this thesis has been prepared in journal format, there is some redundancy between chapters. Chapters 2 and 3 will be submitted to peer-reviewed journals for publication in the near future. Chapter 4 is entitled “Methods for Distinguishing Aspen Seedlings from Suckers in the Field” and was published in the *Journal of Forestry* in 2020. Each chapter has been or will be published with co-authors; as such, the pronoun “we” is used throughout the thesis.

CHAPTER 1

INTRODUCTION

In contrast to Canada and the eastern U.S. where aspen seedling establishment is considered more common (Landhäusser et al., 2019), aspen seedling regeneration was historically considered quite rare and effectively ignored in the western United States, because seedlings were thought to be unable to establish in hotter, drier climates (Long and Mock, 2012; McDonough, 1979). In recent years, genetic work (Mock et al., 2008) and a number of confirmed instances of seedling establishment (e.g., Williams and Johnston, 1984; Kay 1993; Renkin, Despain, and Clark, 1994; Romme et al., 1997; Quinn and Wu, 2001; Fairweather, Rokala, and Mock, 2014; Krasnow and Stephens, 2015; Gill et al., 2017) have contributed to the growing consensus that sexual reproduction is an important component of aspen ecology (Long and Mock, 2012). Aspen seedlings are of particular interest because unlike suckers, seedlings enable species adaptation to climate change through increased genetic diversity and subsequent natural selection, and by facilitating migration with long-distance seed dispersal (Landhäusser et al., 2019).

However, information on aspen seedling frequency as well as factors influencing aspen sexual regeneration is limited, due to historical assumptions of aspen seedling rarity as well as difficulty identifying sexual aspen seedlings from asexual sucker regeneration. While individual studies have identified patterns in seedling establishment in their study sites, inferences are frequently regional or anecdotal (Landhäusser et al., 2019). As a result, we lack even a basic understanding of how common seedling establishment truly is in the western U.S., and by extension, how important a role it plays

at broad scales. Additionally, factors controlling survival and growth of seedlings are not well understood. In particular, the assumption that seedling establishment is largely reliant on favorable, or wetter than average, years, has not been tested.

This thesis addresses several of these knowledge gaps in aspen seedling establishment ecology. Chapter 2 utilizes historical aspen seedling occurrences in the western U.S. and a systematic field survey of 2018 fire footprints to explore patterns and test assumptions of aspen seedling establishment across multiple geographic scales. Specifically, we ask 1) Is aspen seedling establishment restricted to wetter parts of aspen's western U.S. climate envelope? 2) Within a given disturbance, what factors influence seedling establishment probability and how does the establishment probability of seedlings compare to that of suckers? 3) Are seedlings more likely to establish in wetter years than average and does this vary based on a site's climate?

Chapter 3 is a more in-depth investigation of a single widespread post-fire aspen seedling establishment event in southern Utah, identifying and tracking seedlings through time to better understand factors that influence seedling success across a range of elevation, vegetative competition, burn severity, and climate. We ask 1) Where do seedlings establish at both the landscape and microsite level, and what factors explain seedling abundance across the landscape? 2) What factors impact seedling survival and growth once established?

Chapter 4 provides an applied framework for managers and researchers to distinguish aspen seedlings from suckers non-destructively, facilitating future field research into aspen seedling ecology. The chapter is reproduced with permission from a first-authored article published in the Journal of Forestry in 2020. In addition to

presenting several important identifying characteristics, we demonstrate the high accuracy of these methods with field data. These methods also underpin Chapters 2 and 3, and provide confidence in our ability to accurately identifying aspen seedlings in sites across the Intermountain West.

Together, this thesis addresses knowledge gaps of western U.S. aspen seedling ecology at multiple scales—from microsite level to region-wide patterns—and provides applied tools to promote additional research into the many unanswered questions in this understudied aspect of aspen ecology.

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CHAPTER 2

PATTERNS OF ASPEN SEEDLING ESTABLISHMENT IN HISTORICAL AND SYSTEMATICALLY SURVEYED SITES IN THE WESTERN U.S.[1]

Abstract

Sexual establishment is increasingly recognized as an important regeneration pathway in aspen forests in the western U.S., a region previously thought to be too dry for seedling establishment except for during unusually wet periods. Information on aspen seedling establishment and factors influencing its occurrence is limited and frequently anecdotal. Utilizing historical aspen seedling occurrences in the western U.S. and a systematic field survey of 2018 fire footprints, we identified patterns of aspen seedling establishment across multiple scales. Documented seedling establishment has occurred across aspen's western U.S. geographic range, and across much of aspen's western climate envelope. We found seedling establishment in 12 of 15 (80%) fire footprints surveyed, although densities were mostly low. Establishment probability was positively associated with mean annual precipitation and negatively associated with seed-source distance and the density of aspen suckers. Contrary to historical assumptions, we found that documented seedlings have established more often in years that are drier than average. Our results also suggest that aspen seedling establishment may be a widespread, if often low-density, feature in post-disturbance areas. Even in low numbers, aspen seedlings can play a disproportionately large role in aspen regeneration ecology, providing adaptive capacity and facilitating local range expansion.

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[1] Additional co-authors: Larissa L. Yocom

Introduction

Quaking aspen (*Populus tremuloides* Michx.) has a vast range across North America, but plays a unique ecological role in montane ecosystems of the interior western United States. There, often as the only deciduous species at upper elevations, aspen provides habitat and forage for a disproportionately large number of plant and animal species (Kuhn et al., 2011; Mills et al., 2000), and maintains high levels of carbon storage relative to conifer forests (Boča and Van Miegroet, 2017). However, as changing climate and fire regimes modify conditions in novel ways, and aspen in parts of its range experience dieback (Rehfeldt et al., 2009), persistence of aspen is contingent upon survival and regeneration in potentially hotter and drier conditions and the ability to track suitable conditions across a landscape (Davis et al., 2019; Rogers et al., 2020).

Aspen is one of the few species in western montane forests that can reproduce both sexually, through seed, and asexually, through vegetative suckering (Weigle and Frothingham, 1911). Asexual reproduction is advantageous in many scenarios, allowing individual stems, or suckers, to make use of large shared root systems and quickly and vigorously resprout after disturbance (Frey et al., 2003). However, asexual regeneration does not allow for genetic recombination, and a lack of genetic diversity may limit species' adaptability to changing conditions (Hoffmann and Sgrò, 2011). Suckering is limited to locations of existing root systems, thus constraining the velocity with which aspen can migrate. However, aspen's small, wind-dispersed seeds can travel well over 10 km (Turner et al., 2003), offering a mechanism for the species to undergo rapid range shifts as well as recolonize areas where aspen has been lost. Reproduction from seed also increases genetic diversity in a population by recombining genetic material from parent

trees, allowing for the possibility of increased adaptation to future conditions through the selection of individuals with adaptive traits (Mock et al., 2008).

While sexual regeneration is a beneficial regeneration pathway in theory, it is unknown how common seedling establishment truly is in the western U.S. In contrast to Canada and the eastern U.S. where aspen seedling establishment is considered more common (Landhäusser et al., 2019), the prevailing assumption in the western U.S. throughout much of the 20th century was that sexual reproduction in aspen was exceedingly rare. Because aspen seeds are poorly provisioned with little or no endosperm (Karrenberg et al., 2002), and seed viability drops precipitously after several weeks (McDonough, 1979), seeds were thought to require exacting conditions met soon after seed fall, including: 1) bare mineral soil; 2) a relative lack of competing vegetation; and 3) suitably moist soil (Einsphar and Winton, 1976; McDonough, 1979; Weigle and Frothingham, 1911). While the first two requirements are frequently met in post-fire environments, climate in the western U.S. was thought to be prohibitively dry for aspen seedling establishment compared to other parts of aspen's range where seedlings were more commonly found (Faust, 1936; Kay, 1993). Early work on aspen regeneration in the western U.S. acknowledged that seed-based reproduction logically must occur, at least occasionally, in order to explain aspen's range and colonization of new patches (Baker, 1925; Pearson, 1914), however, attempts to find seedlings were unsuccessful (Baker, 1918; Pearson, 1914). Despite reports of aspen seedlings in the subsequent decades (Dixon, 1935; Ellison, 1943; Faust, 1936; Larson, 1944), the narrative solidified into absolute statements during the mid-twentieth century, such as those claiming that aspen "reproduce only through vegetative means [in Utah]" (Cottam, 1954), and are "unable to

reproduce by seed in the Front Range [of Colorado]" (Marr, 1961).

Several occurrences of widespread aspen seedling regeneration more recently in the western U.S. (Kay, 1993; Romme et al., 1997; Williams and Johnston, 1984), along with genetic lines of evidence suggesting recent seedling establishment (Mock et al., 2008), have led to our current understanding that sexual regeneration is more common than once thought (Long and Mock, 2012). However, information regarding seedling regeneration ecology in the western U.S. remains limited and is frequently anecdotal (Landhäusser et al., 2019; Long and Mock, 2012), with few published studies describing naturally occurring aspen seedling establishment. Aspen seedlings can be difficult to distinguish (Kreider et al., 2020), and regenerating aspen stems are frequently assumed to be exclusively aspen suckers, either consciously (McIlroy and Shinneman, 2020) or without any mention of the possibility of sexual regeneration (Pelz and Smith, 2018; Rhodes et al., 2018). As a result, accounts of seedling establishment that do exist in the literature are nearly all serendipitously identified (i.e., researchers or managers happened to observe seedlings but did not set out to do so initially). Furthermore, these accounts document only where aspen seedlings were observed, not where they were absent, making inference about seedling distribution and frequency difficult.

Several studies describing aspen seedling establishment anecdotally link the occurrence of seedlings to above-average precipitation in the year of establishment (e.g., Kay, 1993; Quinn and Wu, 2001; Romme et al., 1997). However, a statistical link between favorable climate and establishment has not been demonstrated, and other studies have reported seedling establishment across multiple years of intense drought (e.g., Fairweather et al., 2014). Asexual regeneration in aspen has been shown to be

positively linked to above-average precipitation and below-average temperatures (McIlroy and Shinneman, 2020), and growth and survival of adult aspen has been shown to be negatively impacted by warmer temperatures and increased drought, except at high elevations (Hanna and Kulakowski, 2012). Conversely, soil temperature that is too low may constrain growth in aspen seedlings (Landhäusser and Lieffers, 1998), suggesting that whether seedling establishment is likely to occur in wetter/cooler or drier/hotter years than average may depend on average climate in a particular site. For example, in hotter, more arid parts of aspen's climate envelope, seedling establishment may be more likely in wetter and/or cooler years, whereas in cooler or wetter parts the reverse may be true. However, no studies have explored patterns of aspen seedling establishment beyond a single, localized site, making it difficult to infer spatial patterns of establishment climate across aspen's entire climate envelope.

Over a hundred years ago, aspen researchers wrote that "just what the proportion of suckers to seedlings is remains an unsolved problem" (Weigle and Frothingham, 1911). Today, the prevalence of aspen seedlings in the western U.S. is still largely unquantified (Landhäusser et al., 2019). In this study, we assembled accounts of historical aspen seedling occurrences in the western U.S. and conducted a systematic field survey of recent fire footprints across a latitudinal gradient in the Intermountain West to quantify predictors of aspen seedling presence and absence. We used these complementary datasets to identify patterns of aspen seedling establishment across multiple scales. Specifically, we asked: 1) Is aspen seedling establishment restricted to wetter parts of aspen's western U.S. climate envelope? 2) Within a given disturbance, what factors influence seedling establishment probability and how does the establishment

probability of seedlings compare to that of suckers? 3) Are seedlings more likely to establish in wetter or cooler years than average and does this vary based on the climate of a site?

Methods

Data

Historical aspen seedling occurrences

We searched for published accounts of quaking aspen seedling establishment in the western U.S. (WA, OR, CA, NV, ID, MT, WY, UT, CO, AZ, and NM) using Google Scholar (https://scholar.google.com) and the Utah State University Aspen Research collection (https://digitalcommons.usu.edu/aspen/). Though aspen occurs in Mexico, a lack of data on seedling establishment in this part of its range restricted our focus to the U.S. alone. We also solicited accounts from researchers and land managers, through a newsletter of the Western Aspen Alliance. In addition to occurrences quantitatively documented in published studies, we identified occurrences that were mentioned in papers but never quantitatively measured (e.g., "I also discovered numerous aspen seedlings in northern Idaho, predominantly on recently burned sites."; Barnes, 1966). In these cases, when possible, an author of the paper was contacted to gain further information. For each account, we recorded the year and type of disturbance which preceded establishment, years in which establishment was reported to have occurred, and the location of the disturbance. Since locations were reported with varying levels of precision, we also grouped accounts into 1) those with "well-characterized" locations (where establishment location could be accurately determined to within a 4-km pixel) and

2) those with vague location descriptions where we could not confidently pinpoint a location. We characterized the observation type of each account as either *quantitative* (sampling plots and/or reported quantitative measurements on seedling abundance, density, or survival) or *descriptive* (distinct aspen seedling occurrences reported or alluded to but no report of detailed quantitative measurements). Though seedlings were surveyed with inconsistent methods across accounts, we characterized the approximate abundance of seedling establishment for each account as *abundant* (numerous seedlings and/or occurring across wide spatial scales within a site) or *sparse* (less than 20 seedlings reported). Seedlings occurring within one disturbance footprint were considered a single occurrence (site). We did not include one account where seedlings were reported to have died during the initial growing season following seed germination (Fechner and Barrows, 1976). See Table 1 for a summary of all historical seedling establishment sites.

Table 1: Historical occurrences of aspen seedling establishment in the western U.S. Total number of establishment years are shown in parentheses for fires where establishment dates are known. Observations deemed "quantitative" contained sampling plots and/or reported quantitative measurements on seedling abundance, density, or survival, while "Descriptive" observations reported or alluded to distinct aspen seedling occurrences but did not report detailed quantitative measurements. Abundance is difficult to compare across sites, as seedlings were sampled with inconsistent methods, however "abundant" observations had numerous seedlings, while "sparse" observations only recorded a small number of seedlings (exact number, if reported, indicated in parentheses).

	State	Name	Disturbance	Disturbance Year	Well-characterized location?	Establishment Years	Observation Type	Abundance	Described by
1.	California	Silver Creek Fire	Fire	2008	Yes	2009 (1)	Quantitative	Abundant	Krasnow and Stephens 2015
2.	California	Angora Fire	Fire	2007	Yes	not known	Descriptive	Abundant	(Carlson et al., 2010)
3.	Oregon	Bull Fire	Fire	1996	Yes	not known	Descriptive	Sparse	Shirley and Erickson 2001
4.	Oregon	Tower Fire	Fire	1996	Yes	not known	Descriptive	NA	Shirley and Erickson 2001
5.	Idaho	"northern Idaho"	Fire	not reported	No	not known	Descriptive	Abundant	Barnes 1966
6.	Wyoming	South of Cooke City	Road disturbance	Mid-80s	No	not known	Descriptive	Sparse (6-12)	Personal communication, B. Williams
7.	Wyoming	Two fires in Yellowstone NP	Fire	1979	No	not known	Quantitative	Abundant	Renkin et al. 1994
8.	Wyoming	Yellowstone NP	Fire	1988	Yes	1989–1993 (5)	Quantitative	Abundant	Kay 1993; Renkin et al. 1994; Romme et al. 1997; Ripple and Larsen 2001; Turner et al. 2003; Hansen et al. 2016; etc.
9.	Idaho	Lyle Springs Fire	Fire	2018	Yes	2019 (1)	Descriptive	Sparse (1)	Personal communication, P. Rogers
10.	Wyoming	Glade Fire	Fire	2000	Yes	2001 (1)	Quantitative	Sparse	Romme et al. 2005, personal communication, M. Turner
11.	Wyoming	Moran Fire	Fire	2000	Yes	2001 (1)	Quantitative	Sparse	Romme et al. 2005, personal communication, M. Turner
12.	Wyoming	Beaver Creek Fire	Fire	1985	Yes	1986–1989 (4)	Quantitative	Abundant	Kay 1993
13.	Idaho	Wooley Valley Mine	Mine reclamation	1978	Yes	1979 (1)	Quantitative	Abundant	Williams and Johnston 1984
14.	Utah	Wasatch Mountains	None	NA	No	not known	Descriptive	Sparse (5)	Every and Wiens 1971

15.	Utah	Wasatch Mountains	None	NA	No	not known	Descriptive	Sparse (“a group”)	Every and Wiens 1971 (Kimball Harper discovery)
16.	Utah	Strawberry Reservoir	Reservoir drawn down	1924	Yes	1925 (1)	Descriptive	Abundant	Faust 1936; Larson 1944
17.	Utah	Central Utah	None	NA	No	not known	Descriptive	NA	Dixon 1935
18.	Utah	Aquarius Plateau	None	NA	No	not known	Descriptive	Sparse (1)	Ellison 1943
19.	Utah	Brian Head Fire	Fire	2017	Yes	2018 (1)	Quantitative	Abundant	M. Kreider, unpublished data
20.	Arizona	Pumpkin Fire	Fire	2000	Yes	2001–2006 (6)	Quantitative	Abundant	Fairweather et al. 2014
21.	Arizona	Hochderffer Fire	Fire	1996	Yes	1997 (1)	Descriptive	Sparse	Personal communication M. Fairweather
22.	Arizona	Schultz Fire	Fire	2010	Yes	2011 (1)	Quantitative	Abundant	Fairweather et al. 2014
23.	Arizona	KP Fire	Fire	2004	Yes	not known	Descriptive	Abundant	Fairweather et al. 2014; Personal communication, E. Margolis
24.	Arizona	Wallow Fire	Fire	2011	Yes	2012 (1)	Descriptive	Abundant	Fairweather et al. 2014; Personal communication M. Fairweather
25.	Arizona	Thomas Fire	Fire	2003	Yes	not known	Descriptive	Abundant	Fairweather et al. 2014; Personal communication, E. Margolis
26.	Arizona	Rattlesnake Fire	Fire	1994	Yes	1996–1998 (3)	Quantitative	Abundant	Quinn and Wu 2001
27.	New Mexico	Las Conchas Fire	Fire	2011	Yes	2013 (1)	Descriptive	Abundant	Personal communication, P. Rogers, J. Jacobs
28.	Colorado	West Fork Complex	Fire	2013	Yes	2014–2018 (5)	Quantitative	Abundant	Personal communication, K. Nigro
29.	Colorado	San Juan Mountains	None	NA	No	not known	Quantitative	Abundant	Elliott and Baker 2004
30.	Colorado	Mt. Zirkle Fire	Fire	2002	Yes	not known	Quantitative	Abundant	Buma and Wessman 2012; Gill et al. 2017

For historical sites with well-characterized locations, we designated a single geographic point, determined from coordinates or other information from accounts. At each point, we extracted long-term average annual mean temperature and precipitation for the thirty-year period of 1981–2010, obtained from 4-km^2 PRISM datasets (PRISM Climate Group, 2019) via Google Earth Engine (Gorelick et al., 2017). For sites with known establishment dates, we also characterized annual and seasonal establishment climate using a suite of attributes shown to impact forest regeneration across the western U.S. These included precipitation, temperature, climate water deficit, vapor pressure deficit, and Palmer Drought Severity Index (Davis et al., 2019; Hankin et al., 2019; Kemp et al., 2019; Korb et al., 2019). Monthly precipitation and mean temperature data were again obtained from PRISM datasets (PRISM Climate Group, 2019), while monthly climate water deficit, vapor pressure deficit, and Palmer Drought Severity Index (PDSI) were obtained from 4-km^2 TerraClimate datasets (Abatzoglou et al., 2018). Climate variables from TerraClimate were not available for one historical site with establishment in 1925 (Strawberry Reservoir).

Aspen seeds generally mature in May or June (Landhäusser et al., 2019), with seeds remaining viable for several weeks after dispersal (McDonough, 1979; Moss, 1938). Given this, we used the window of June–August ("summer") to characterize climate during the window of germination and early growth, and an annual window (water year; preceding October to September of the establishment year) to characterize climate over a longer time period including the prior winter's snowpack. Finally, we also calculated a variety of metrics using June–August daily precipitation data for each establishment site-year. These included: number of days with precipitation (>3 mm

precipitation; Hao et al., 2012); the average length of wet streaks (consecutive days with >3 mm precipitation); and rain intensity (the average amount of rainfall on days where rainfall occurred). Daily precipitation data were obtained from Daymet (Thornton, 2020), a 1-km^2 gridded dataset of daily surface weather data, and accessed via Google Earth Engine (Gorelick et al., 2017).

All site-year climate variables were calculated as anomalies from long-term (1981–2010) site averages, and quantified as z-scores, or the number of standard-deviations a given climate variable fell from the site's long-term average for that variable, given 1981–2010 inter-annual variance. To simplify visual interpretation, we inverted (multiplied by -1) z-scores for climate water deficit and vapor pressure deficit variables. Consequently, z-scores above zero for all precipitation-related climate variables correspond to wetter conditions while z-scores below zero correspond to drier conditions (Table 2). We conducted all data-aggregation in the R statistical software (R Core Team, 2018), and used *tidyverse* packages (Wickham et al., 2019).

Table 2: Summary of establishment site-year climate variables. Annual aggregation windows were a water year (preceding October to September of the establishment year); summer aggregation windows were June–August of the establishment year. Citations for data sources are as follows: PRISM (PRISM Climate Group, 2018); TerraClimate (Abatzoglou et al., 2018); Daymet (Thornton et al., 2016).

Climate variable	Z-scores inverted? (multiplied by -1)	Description	Aggregation windows	Data source	Spatial resolution
Precipitation	No	Total precipitation (mm)	Annual, summer	PRISM	4 km
Temperature	No	Mean monthly temperature (°C)	Annual, summer	PRISM	4 km
Climate water deficit	Yes	Mean monthly climate water deficit (mm)	Annual, summer	TerraClimate	4 km
Vapor pressure deficit	Yes	Mean monthly vapor pressure deficit (kPa)	Annual, summer	TerraClimate	4 km
Palmer Drought Severity Index	No	Mean monthly Palmer Drought Severity Index	Annual, summer	TerraClimate	4 km
Average length of wet streaks	No	Average length of consecutive days with >3 mm precipitation	Summer	Daymet V3	1 km
Rain intensity	No	Average amount of rainfall on days where rainfall occurred	Summer	Daymet V3	1 km
Number of days with precipitation	No	Number of days with >3 mm precipitation	Summer	Daymet V3	1 km

Systematic aspen seedling occurrences

To systematically quantify aspen seedling establishment in recently burned areas, we first defined a search area, from the north rim of the Grand Canyon to the northern Wyoming border, within the rectangle formed from -114° to -109° longitude and 36° to 44° latitude (Figure 1). Within this area, using the Historic Fire Database (Weber, 2020) we identified wildfires that burned in 2018 1) over 50 acres; 2) on U.S. Forest Service public land, and 3) in areas that contained pre-fire aspen, determined using online photographs of fire footprints from InciWeb (https://inciweb.nwcg.gov/) in conjunction with pixels modeled by the National Individual Tree Species Atlas as containing aspen (Ellenwood et al., 2015). We chose fires which burned in 2018 to allow for time for

seedling establishment to potentially occur prior to sampling, and before seedlings and suckers became indistinguishable (Kreider et al., 2020).

Within each fire perimeter, we defined an "area of interest" (AOI) in which to locate plots. These areas 1) burned (dNBR > 100; Parks et al., 2018) and 2) contained forest vegetation prior to the fire (i.e., excluding meadows and sparsely vegetated slopes). Using the R statistical software (R Core Team, 2018), we generated plot locations in this AOI, with the number of plots per fire a function of the size of the AOI. In fire footprints with trail or road access, we randomly placed plots in a band 30–100 m away from the trails and roads. In fire footprints without trails or roads, plots were placed randomly within AOIs. Plots in all fires were placed ≥50 m from the edge of the fire perimeter and ≥ 200 m from another plot. Sampling occurred from June–August 2020 in 15 fires, spanning 900 km north to south. Due to time constraints, we did not visit two fire areas (Cobblerest and Crooked Creek), both of which were under 200 acres in size. A summary of site characteristics can be found in Table 3.

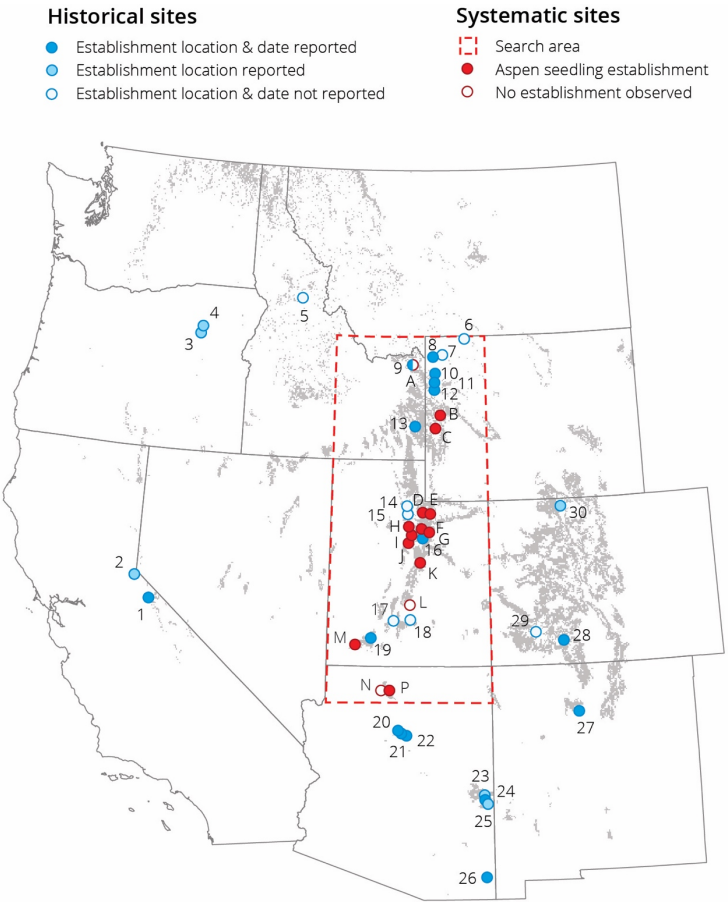

Figure 1: Map of historical and systematic sites in the western U.S. Locations for historical sites without well-characterized location information (Table 1) were estimated. Aspen distribution is shown in grey, created using National Individual Tree Species Atlas; Ellenwood et al., 2015). See Table 1 and Table 2 for historical and systematic site characteristics, respectively.

Table 3: Systematic site characteristics. All fires burned in 2018. We report size of each fire footprint's "Area of Interest" instead of the total footprint size, since some fires had large areas that did not meet our search requirements (e.g., not forested pre-fire or forest vegetation was composed only of low-elevation tree species such as Pinyon-Juniper woodlands).

	Fire footprint	State	Area of Interest size (ha)	Total plots	Occupied plots	Mean|median|max seedlings ha^{-1} in occupied plots	Elevation min–max (m)	Elevation range (m)	Annual precipitation (mm)	Annual temperature (°C)
A.	Lyle Springs	Idaho	15	4	0 (0%)*	—	1879–1883	4	648	3.5
B.	Roosevelt	Wyoming	13992	60	3 (5%)	100 | 100 | 100	2244–2920	676	467–1013	1.3–2.0
C.	Marten Creek	Wyoming	2047	24	2 (8%)	100 | 100 | 100	2246–2915	669	839–1098	0.3–2.5
D.	Slate	Utah	112	5	1 (2%)	100	2957–3084	127	1060–1111	2.7
E.	Murdock	Utah	1719	23	14 (61%)	900 | 2500 | 9700	2522–3074	551	846–986	1.4–3.3
F.	Willow Creek	Utah	422	17	5 (29%)	100 | 300 | 900	2506–2707	201	816–892	3.9–4.2
G.	Dollar Ridge	Utah	4350	27	6 (22%)	100 | 100 | 200	2717–3096	384	687–809	2.3–4.0
H.	Coal Hollow	Utah	4990	39	1 (3%)	700	2334–2696	362	572–761	4.6–5.9
I.	Pole Creek	Utah	11883	25	1 (2%)	100	2272–2731	459	669–791	4.4–6.3
J.	Bald Mountain	Utah	5588	27	0 (0%)†	—	2126–2637	511	651–819	5.0–7.8
K.	Trail Mountain	Utah	4908	24	5 (21%)	200 | 1000 | 4500	2283–3148	864	499–1000	2.0–5.8
L.	Pole Canyon	Utah	63	11	0 (0%)	—	2925–3114	190	616–687	3.0–4.2
M.	West Valley	Utah	3364	19	0 (0%)†	—	2283–2719	436	635–769	5.8–7.3
N.	Stina	Arizona	90	12	0 (0%)	—	2336–2434	99	583–600	8.1–8.6
P.	Cat	Arizona	206	12	3 (25%)	100 | 100 | 100	2655–2776	121	599–703	6.2–7.5
				329	**41 (12%)**	**100 | 1100 | 9700**	**1879–3148**	**1269**	**467–1111**	**0.3–8.6**

*An aspen seedling was observed within the Lyle Springs fire footprint in 2019 (P. Rogers, personal correspondence). †Seedlings were found in the fire area, however not in any plots.

Each plot consisted of a 50x2 m belt transect, established parallel to slope contours. This search area was chosen to be the most informative plot size for presence-absence sampling (Ståhl et al., 2017), based on median densities of aspen seedlings at another post-fire site in southern Utah (Chapter 3). Plots spanned a range of forest vegetation. In addition to quaking aspen (*Populus tremuloides*) which occurred in or proximal to all plots by design, pre-fire vegetation consisted largely of pinyon pine (*Pinus edulis*) and juniper (*Juniperus osteosperma* and *Juniperus scopulorum*) woodlands at lower elevations; ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), and white fir (*Abies concolor*) at mid-elevations; and subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and limber pine (*Pinus flexilis*) present at higher elevations. Additionally, lodgepole pine (*Pinus contorta*) was dominant in many plots at higher latitudes.

In June–August 2020, we systematically searched each plot for the presence of aspen seedlings. If present, we also recorded the number of seedlings encountered. Aspen seedlings were identified non-destructively using methods detailed by Kreider et al., (2020), which demonstrated 96% predictive accuracy in aspen stems two years post-fire . The first aspen seedling to be found in each fire footprint was excavated in order to definitively verify that aspen seedlings were present in the area. We deposited these seedlings at the Intermountain Herbarium at Utah State, where they can be viewed in person or online at http://intermountainbiota.org (example catalog number: UTC00286626; to see all samples, set “Collector’s Last Name” as “Kreider” in the catalog search). We also scanned for aspen seedlings while traveling between plots. Fires were considered to have aspen seedling occupancy even if seedling establishment was

only observed outside of plots.

At each plot we recorded sub-meter coordinates and elevation. At the plot center, we recorded the distance to the nearest live aspen tree of reproductive age using a laser rangefinder and estimated pre-fire overstory basal area by species using a 10 basal area factor wedge prism. We divided plots into 50 1x2 m subplots, and recorded the presence of burned soil in each subplot. To obtain information about intraspecific competition, we recorded the presence of aspen suckers in each subplot along the transect. We also quantified herbaceous vegetation using photos of the transect, taken facing inwards from each end. For each photo, we assigned one of the following values: 1. virtually bare ground along the transect with no competing vegetation; 2. mostly bare ground with some sporadic vegetation; 3. relatively similar amounts of bare ground and vegetation; 4. mostly covered with vegetation, but with some visible areas of bare ground; or 5. thick vegetation along virtually all parts of transect. Plots were assigned the average of values of both photos. We calculated live canopy cover percentage every 10 m along the transect, and assigned each plot the average of these six measurements. We extracted slope, and calculated sin-transformed aspect (Beers et al., 1966) and differenced Normalized Burn Ratio (dNBR) in Google Earth Engine from USGS National Elevation and Sentinel datasets respectively (Gorelick et al., 2017; Parks et al., 2018). We obtained 30-year climate normals (1981–2010) of yearly precipitation and mean temperature for each site from PRISM 800m datasets (PRISM Climate Group, 2019). We did not attempt to age seedlings to determine the year in which each established. Though the majority of seedlings likely established one year following fire in 2019, establishment could have occurred in 2018, 2019, and/or 2020 (prior to sampling).

Analysis

Seedling establishment vs. western aspen climate envelope

To describe the climate envelope of quaking aspen in the western U.S., we created 10,000 randomly-selected points within its geographic distribution in the western U.S. (pixels containing aspen modeled by the National Individual Tree Species Atlas; Ellenwood et al., 2015). At each point, we determined long-term average annual mean temperature and precipitation for the thirty-year period of 1981–2010. Climate data were obtained from 4-km^2 PRISM datasets (PRISM Climate Group, 2019) via Google Earth Engine (Gorelick et al., 2017). In order to assess whether aspen seedling establishment is restricted to certain parts of aspen's western U.S. climate envelope, we compared this climate envelope to the average annual mean temperature and precipitation of historical sites (subset to those with precisely known locations, n = 22) and systematic sites with seedling establishment.

Factors influencing seedling establishment occupancy

We used a Bayesian framework to model occupancy of aspen seedlings in plots within systematic sites. Examining correlations between predictor variables, elevation and latitude were highly correlated with annual precipitation and mean temperature. Since climate is a more ecologically meaningful driver of seedling establishment, we retained precipitation and temperature predictors and removed elevation and latitude from the analysis. We scaled and centered predictors (Table 4) and fit a binomial generalized linear model:

$$\text{seedling site occupancy} \sim bernoulli(p)$$

$$\begin{aligned} logit(p) = \alpha + \beta_1 \times \text{dNBR} + \beta_2 \times \text{burn} + \beta_3 \times \text{slope} + \beta_4 \times \text{aspect} \\ + \beta_5 \times \text{canopy cover} + \beta_6 \times \text{seed-source distance} + \beta_7 \times \text{suckers} \\ + \beta_8 \times \text{herbacious competition} + \beta_9 \times \text{annual precipitation} \\ + \beta_{10} \times \text{annual temperature} \end{aligned}$$

where p is probability of occupancy, α is the intercept term and β_x values are slope coefficients. We used uninformative priors, modeling $\alpha \sim normal(0, 1.5)$ and all slope parameters as $\beta \sim normal(0, 3)$. We also fit an identical model with the addition of an interaction between annual precipitation and temperature and calculated the Widely Applicable Information Criteria (WAIC) value for each model to determine which model explained more variance. Finally, we fit a similar model with plot sucker occupancy as the response variable, to compare modeled rates of sucker vs. seedling occupancy; in this model we removed sucker density as a predictor variable. We fit all models using the *ulam* function in the *rethinking* package (McElreath, 2020) in R (R Core Team, 2018). This package interfaces with the *rstan* package to fit Stan models using Hamiltonian Monte Carlo (Stan Development Team, 2020). We ran each model with four chains of 4,000 samples, 1,000 of which were warmup. We verified model convergence using Gelman-Rubin convergence diagnostics (Gelman and Rubin, 1992) and by visually inspecting parameter trace plots.

Table 4: Summary of predictors in the systematic plot occupancy model. Mean and range are for the un-scaled data.

Predictor	Description	Mean	Range
dNBR	Differenced normalized burn ratio (scaled by 10^3)	331	-303–974
Burn	Percent of 1x2 m subplots containing burned ground	95 %	10–100 %
Slope	Slope in degrees (remotely sensed from 1/3 arc second Digital Elevation Model)	15°	1–34°
Aspect	Sin-transformed folded aspect; 0 = NE, 2 = SW (remotely sensed from 1/3 arc second Digital Elevation Model)	1.04	0–2
Canopy cover	Live vegetation canopy cover percentage	4 %	0–79 %
Seed-source distance	Distance from plot center to nearest live aspen tree of reproductive age	464 m	0–1600 m
Suckers	Percent of 1x2 m subplots containing aspen suckers	17 %	0–100 %
Herbaceous competition	Photo-derived level of plot herbaceous vegetation; 1=very low, 2=low, 3=medium, 4=high, 5=very high	3.1	1–5
Annual precipitation	1981-2010 normal annual total precipitation (800 m pixel)	752 mm	467–1111 mm
Annual temperature	1981-2010 normal annual mean temperature (800 m pixel)	4.0°C	0.3–8.6°C

To interpret model results, we calculated posterior means of each parameter, as well as the probability that each posterior was above or below zero, depending on the sign of the mean. We also characterized uncertainty in the posterior through "compatibility intervals" around the mean (Amrhein et al., 2019; McElreath, 2020). We adopt this wording—instead of "confidence" or "credibility" intervals—to caution against overconfidence in interpretation, remembering that estimates come from models that are always incomplete and imperfect; thus results from models can be described, at best, as "compatible" with the *model* (Amrhein et al., 2019). Furthermore, we remind the reader that any chosen interval percentile (e.g., 50%, 89%, or 95%) is inherently arbitrary and values outside this interval are not incompatible, just less compatible. When possible, we have presented the full posterior instead of intervals, in order to more clearly convey

uncertainty in estimates.

Climate in the year of establishment

To determine whether seedlings were likely to establish in wetter years than average and if this varied based on a site's climate, we used historical sites where establishment dates were known (n = 16). We did not include systematic sites in this analysis, because all systematic fires occurred in the same year, and they shared similar post-fire inter-annual climate. For the 16 historical sites with known establishment years, each year with aspen seedling establishment was treated as an independent data point; thus the unit of observation is a site-year. We used a Bayesian framework to model the mean of climate z-scores in years of establishment. We also included linear predictors to assess whether a historical site's normal 1981–2010 precipitation and temperature influenced the climate in which seedlings established. We scaled and centered 1981–2010 precipitation and temperature linear predictors so that the intercept α represented the overall mean of establishment-year z-scores for each climate response variable. For response variables aggregated at the annual scale, we used annual precipitation and temperature normals as the predictors, and we used summer normals as the predictors for models in which the response variable was aggregated at the summer scale. We fit the following linear model for each climate response variable:

$$\text{establishment z-scores} \sim Normal(mu, sigma)$$
$$mu = \alpha + \beta_1 \times normal\ precipitation + \beta_2 \times normal\ temperature$$

We used weakly informative priors, assigning α the prior $\alpha \sim Normal(0, 1)$ given our expectation that z-scores would be centered close to 0 like historical site 1981–

2010 z-scores. The variance parameter, $sigma$, was assigned the prior $sigma \sim Exponential(1)$ since standard deviation was expected to be roughly 1. β parameters were assigned the prior $\beta \sim Normal(0, 1.5)$, covering virtually all possible potential parameter estimates (because predictors were scaled and establishment z-scores were also on a standardized scale). We fit models using the *ulam* function in the *rethinking* package (McElreath, 2020) in R (R Core Team, 2018), and assessed model convergence as before.

Results

The literature search and solicitation for information from aspen professionals returned 30 historical occurrences of aspen seedling establishment in the western U.S. (Table 1). The earliest documented aspen seedling establishment occurred in 1925 (Faust, 1936; Larson, 1944) and published reports of additional seedling establishment have occurred nearly every decade since. Historical occurrences span much of aspen's geographical range in the western U.S. and do not appear to be restricted to specific regions (Figure 1). Occurrences were largely associated with post-disturbance environments, with 71% of occurrences following fire, 11% after human-caused disturbances, and the remaining 18% of occurrences had either no obvious disturbance or it was unknown whether a disturbance had occurred. While several of the occurrences contained only one or a few seedlings (Ellison, 1943; Every and Wiens, 1971), the majority of documented occurrences contained extensive seedling establishment which generally occurred across large areas of a disturbance. Seedling occurrences that followed fire tended to be extensive and widespread, while occurrences not associated with a

disturbance event tended to be isolated and limited to a few seedlings. Of the 16 occurrences for which establishment years were known, 11 had documented establishment in only a single year. In the remaining five, seedlings established across multiple, consecutive years ranging from three to six years in a row (e.g., Fairweather et al., 2014; Kay, 1993; Romme et al., 1997). In sites with multiple years of seedling establishment, most seedlings established in years shortly after the disturbance, with continued, but declining, establishment numbers in the following years (Appendix A). In total, there were 34 site-years with aspen seedling establishment.

We found aspen seedling establishment in 12 of the 15 recent fires (80%) that we systematically surveyed. All three fire footprints in which we did not observe aspen seedlings were small, with relatively few plots surveyed (Table 3). In one of these (Lyle Springs), researchers documented a single aspen seedling in 2019 (P. Rogers, personal correspondence), however we did not observe any seedling establishment in our sampling. Across all fires, 41 of 329 plots had seedling establishment (12%). Of these occupied plots, 22 (54%) had no pre-fire aspen (i.e., the plot had no measured live or dead aspen basal area nor any resprouting suckers). The median distance of occupied plots to the nearest aspen seed source (live tree of reproductive age) was 205 m, however 8 plots with seedling establishment were at least 1 km from the nearest observed seed source. Within fires, plot occupancy percentage varied greatly, with some fires having only a single plot occupied while others having over 60% of plots occupied (Table 3). Seedling densities in occupied plots spanned a large range; the median number of seedlings was 1 (per 100 m^2 plot), however we observed much higher densities in several fires, up to nearly 100 seedlings in one plot (Table 3).

Seedling establishment vs. western aspen climate envelope

Twenty-two historical sites had well-characterized locations, along with the 329 plots within systematic sites, allowing for comparison of average 1981–2010 annual climate between sites with aspen seedling presence/absence and the overall climate envelope of aspen in the western U.S. Sites with seedling establishment spanned a wide range of average annual mean temperature (0.5–9.5° C). Average annual precipitation of establishment sites also covered a large range (533–1192 mm), however there were no sites with seedling establishment in the drier portion of aspen's climate envelope (below 500 mm of average annual precipitation; Figure 2). Seedling establishment occurred in systematic sites with as little as 519 mm of average annual precipitation, however the majority (88%) of systematic sites with seedling establishment occurred above 750 mm of average annual precipitation, even though only 43% of the sampled sites were located in areas with precipitation above that threshold.

Factors influencing seedling occupancy

Logistic binomial regression of systematic sites revealed several predictor variables associated with plot seedling occupancy probability. Annual precipitation had the largest effect size (Figure 3), with increased plot occupancy at sites with higher mean annual precipitation (Figure 2). Modeled seedling occupancy was negatively related to the density of aspen suckers in a plot as well as the distance to the nearest seed source. Fire severity (dNBR) did not appear to have a strong connection to occupancy probability; however, increased amount of burned subplots was positively linked to occupancy probability. Modeled plot occupancy probability was higher as aspect approached SW orientations, and lower as aspect approached NE orientations. Seedling

and sucker occupancy were equivalent in wetter sites, however seedling occupancy decreased more strongly in drier sites (Figure 4).

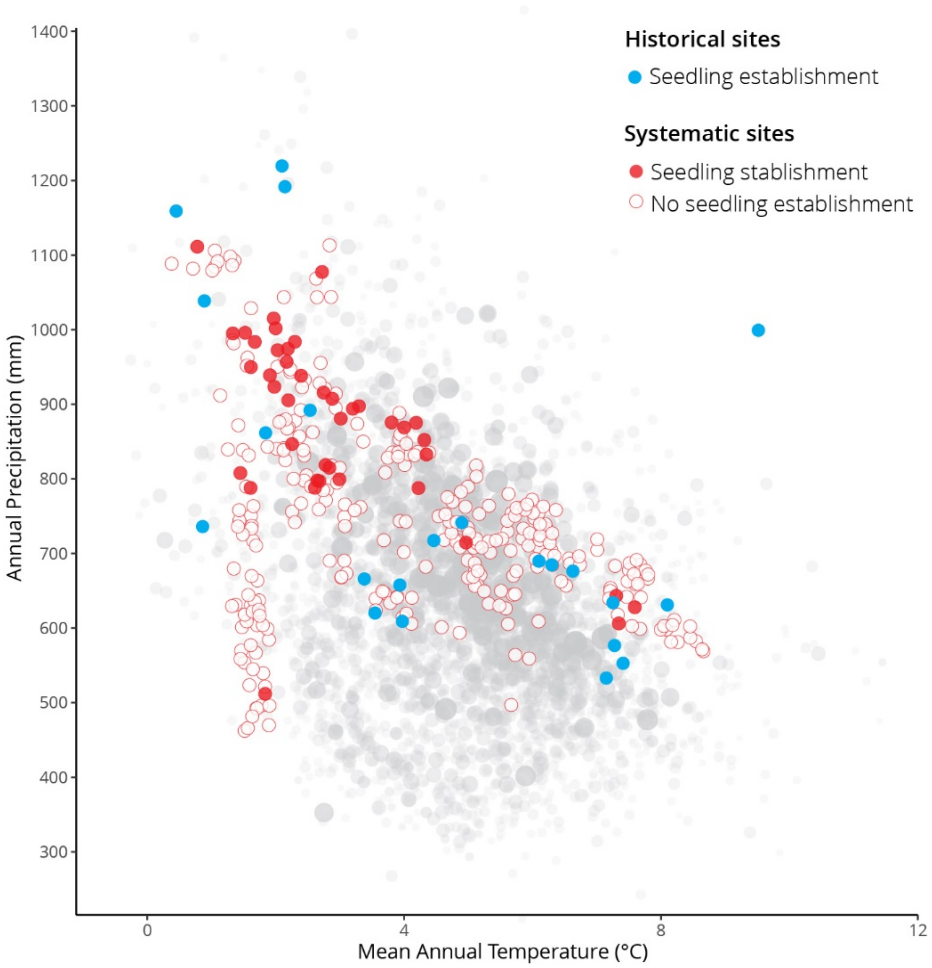

Figure 2: 1981–2010 annual precipitation and temperature normals for historical and systematic sites. Only historical sites with well-characterized locations. Grey points are 1981–2010 normals from 10,000 randomly-selected points within pixels of modeled aspen distribution in the western U.S. (Ellenwood et al., 2015), representing the climatic envelope of current aspen distribution. Size and transparency of grey points are proportional to the modeled basal area of aspen in that pixel.

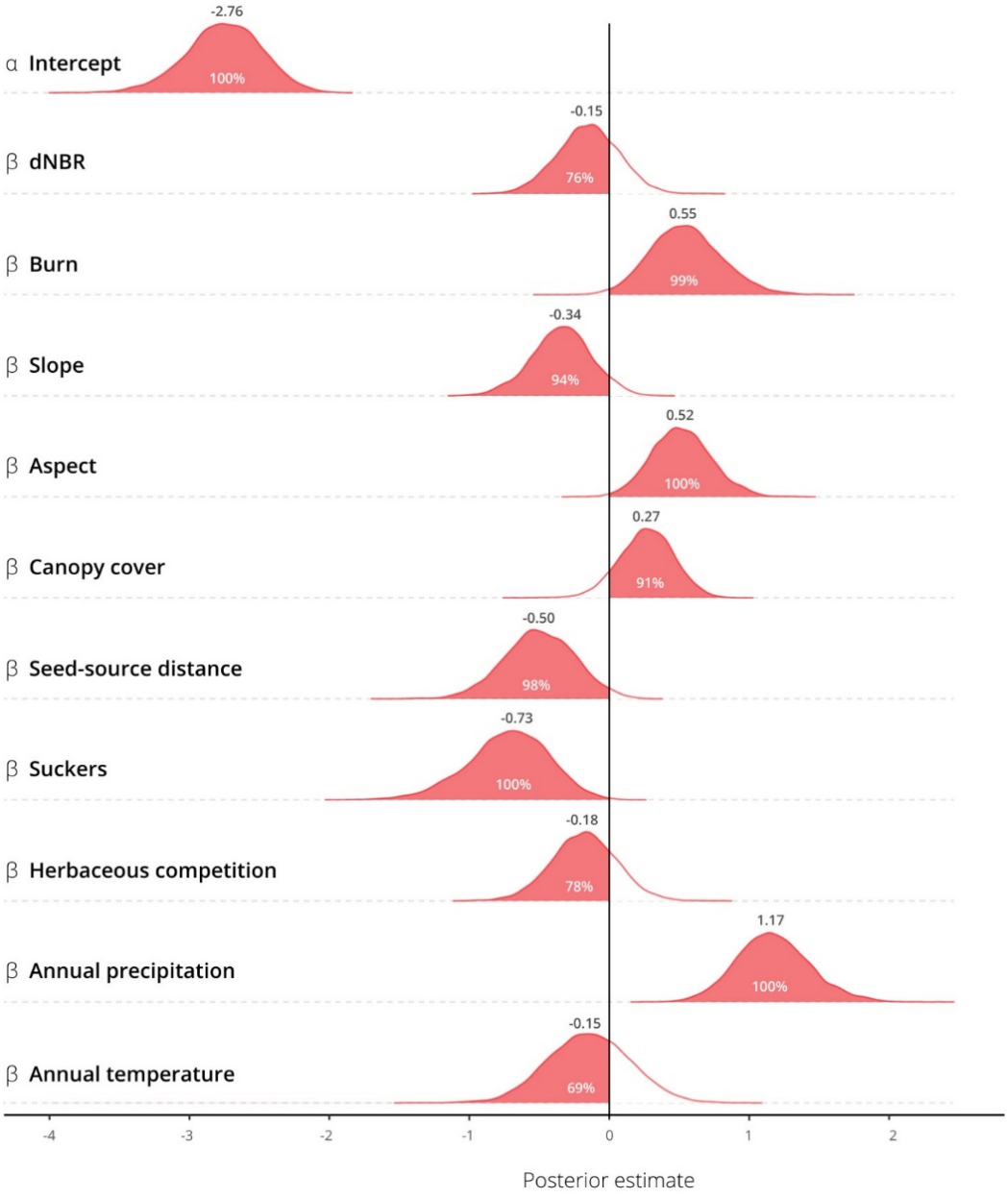

Figure 3: Parameter posterior estimates for the systematic site occupancy logistic generalized linear model. The mean is indicated above each posterior distribution. Area above/below zero (depending on the sign of the mean) is shaded in red; the probability that the true mean (given the data) is positive/negative is indicated in shaded areas.

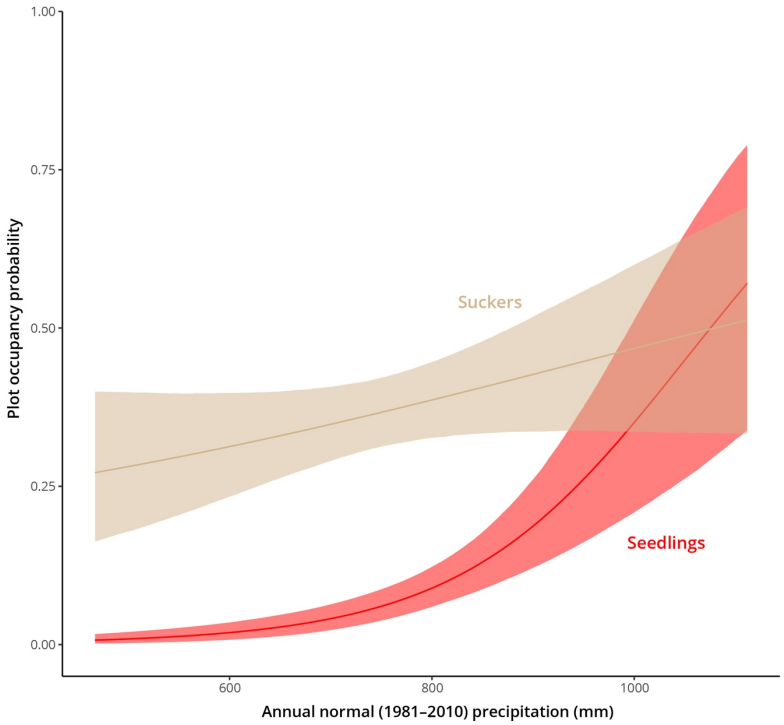

Figure 4: Systematic site modeled occupancy predictions. Predictions shown for seedling (red) and sucker (tan) occupancy as a function of annual precipitation, with 89% credible interval of posterior mean shown for each prediction. All other predictors were held at 0 (their means).

Climate in the year of establishment

Sixteen historical occurrences reported the year(s) in which seedlings established (34 establishment site-years total), which allowed us to explore whether seedlings were more likely to establish in wetter or cooler than average years. Seedlings established in years spanning a wide range of annual and summer climate conditions, from years greater than 2 standard deviations (z-scores) hotter or drier than average, to years greater than 3 standard deviations wetter or cooler than average. Annual precipitation in the year of establishment ranged from less than 300 mm to over 1200 mm of annual precipitation (Figure 5). Though we only display individual values for annual precipitation, other establishment site-year climate variables showed similar trends. The means of overall

intercept (α) estimates were negative (drier/hotter than average) for all climate variables, ranging from 0.08 to 0.55 standard deviations drier or hotter than average 1981–2010 conditions. However, the strength of this trend varied (Figure 6). For example, annual and summer vapor pressure deficit and summer climate water deficit α estimates included significant posterior area of both negative and positive values, indicating little difference in these variables from conditions expected under a random subset of years. On average, years with aspen seedling establishment had fewer summer days with precipitation, shorter streaks of consecutive days of rainfall, and lower rainfall intensity (amount of rain on days when rainfall occurred) than average. Modeled *sigma* posteriors were generally around 1 (Appendix B) as expected, since z-scores arise from a process that centers and scales variables.

We found scant evidence to suggest that climate z-scores varied as a function of normal precipitation or temperature (Appendix B; also see Figure 5). Only two models—annual mean temperature and summer PDSI—had a β parameter posterior in which its 89% compatibility interval did not include 0, and even in these, model predictions were largely hotter and drier than average across the majority of prediction space.

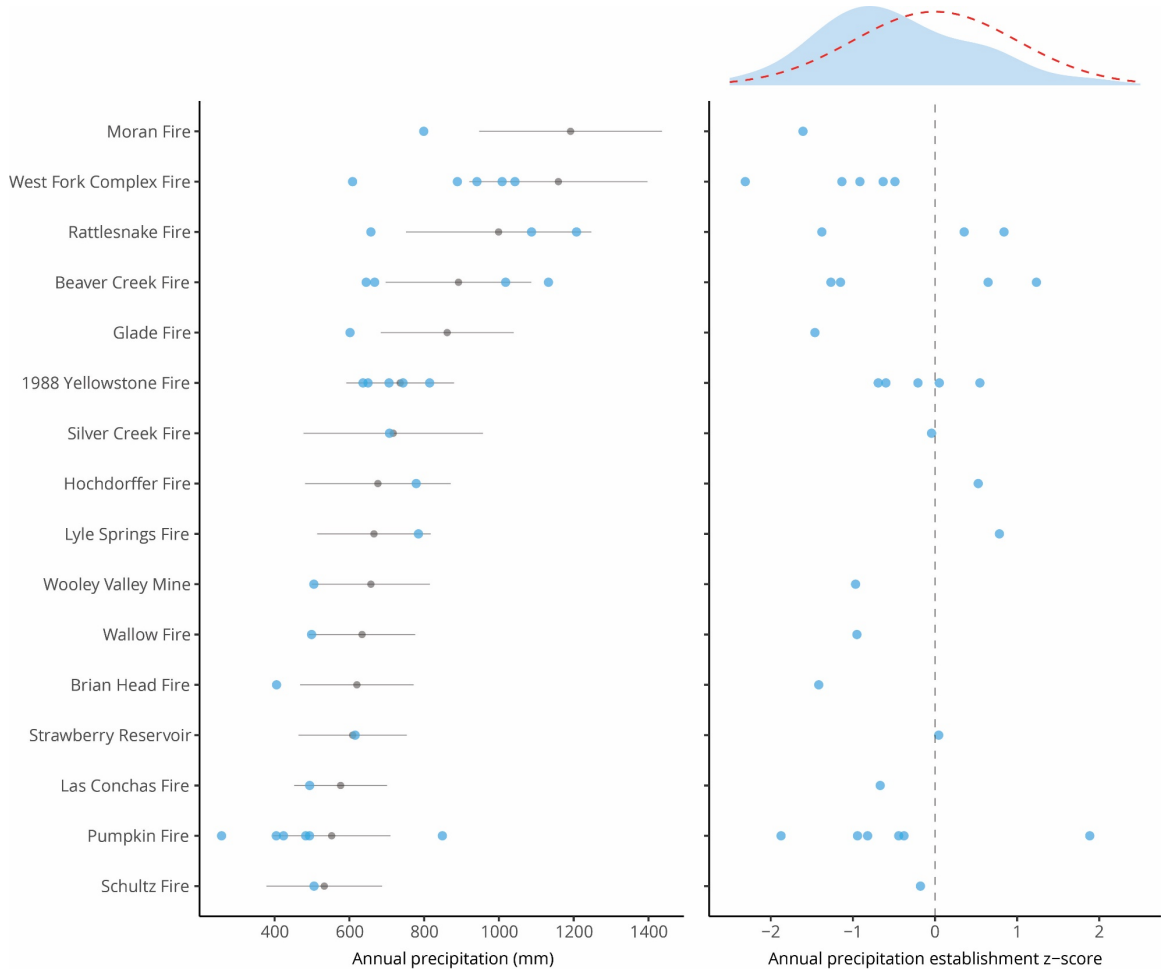

Figure 5: Annual precipitation of establishment site-years. Left: Un-standardized annual precipitation for years of seedling establishment. A site's 1981–2010 average annual precipitation is shown with a grey dot, and one standard deviation with a grey line. Right: Z-scores of annual precipitation for years of seedling establishment. Values below zero represent drier conditions than average. A kernel density estimate of establishment z-scores is shown, as well as the expected density distribution of random z-scores (dotted red line).

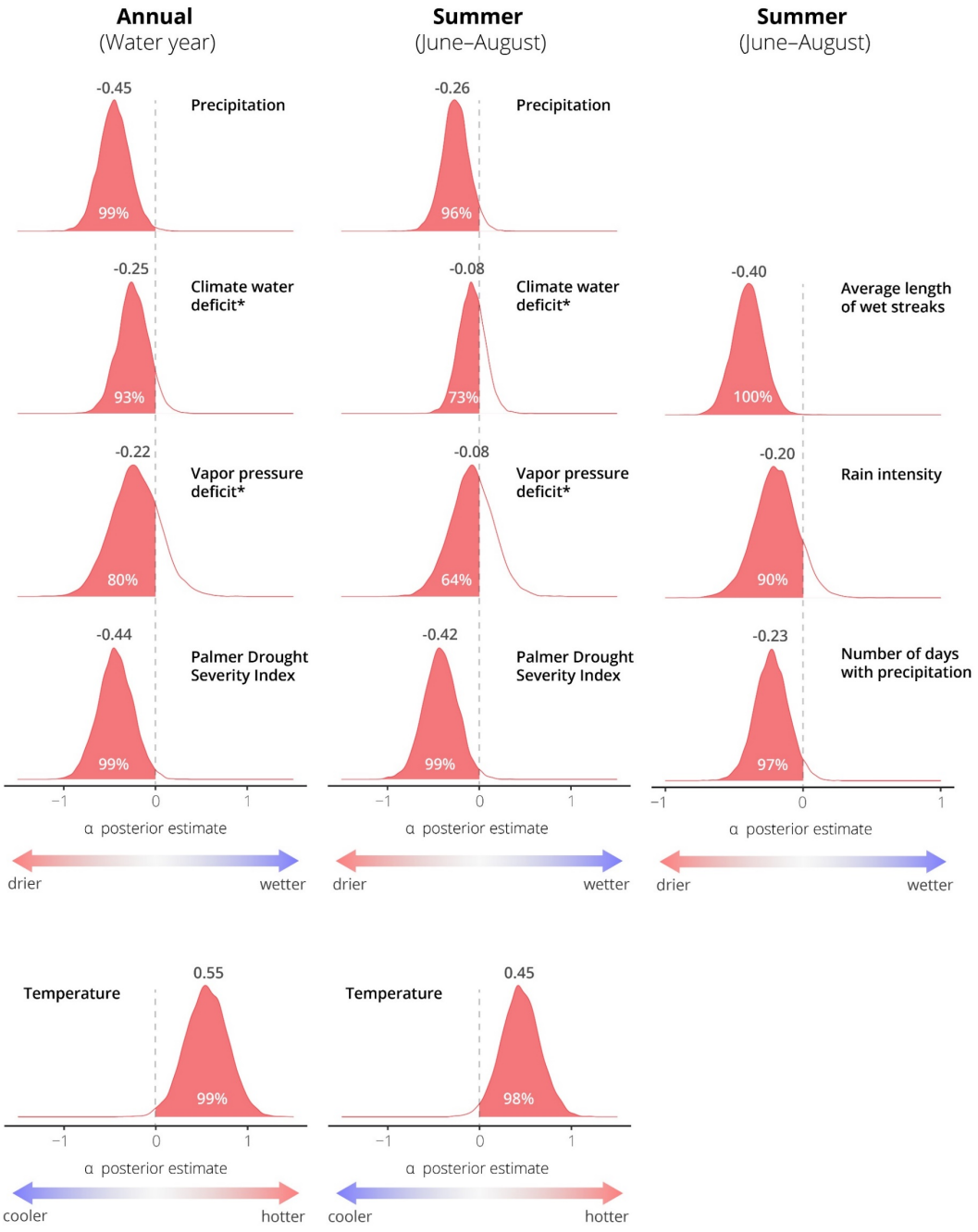

Figure 6: Climate in the year of establishment in historical sites. Intercept (α) posterior estimates for linear models of establishment-year climate variables. Since linear predictors are scaled and centered, α represents the overall mean of establishment z-scores for each variable. Area below/above zero is shaded in red; the probability that the true mean (given the data) is negative/positive is indicated within the shaded area. Posterior means are shown above each distribution. Variables with an asterisk have been inverted (multiplied by -1) so that all precipitation-related variables share a common scale, where positive values represent wetter conditions than average, and negative values represent drier conditions.

Discussion

The aspen seedling establishment that we present here—documented by other researchers and measured in our systematic survey—adds to the growing consensus that aspen seedling establishment is a much more common occurrence than once believed. Historical occurrences of seedling establishment have been documented in geographic areas spanning much of the western U.S., from the northern Rocky Mountains to areas near the Mexican border, where aspen occurs in isolated pockets. Our systematic survey of fires showed that the majority of fire footprints contained at least low levels of seedling establishment. Though we did not observe aspen seedlings in our systematic sampling of the Island Park fire footprint, one seedling was documented in 2019 (P. Rogers, personal correspondence), meaning that only two of fifteen fires surveyed did not have some sort of documented seedling establishment. Both of these fires were small, with few plots surveyed, and it is possible that seedlings were present, however at very low densities that we did not detect.

We show that seedlings can, and have, established across a wide range of temperature and precipitation conditions in the western U.S. However, while historical occurrences demonstrate that seedling establishment can occur in very dry areas of the western U.S. (e.g., years less than 400 mm of annual precipitation; Figure 5), seedling establishment in systematic sites was much more likely in wetter sites, with reduced probabilities below 750 mm of average annual precipitation. Because historical occurrences were serendipitous and provide presence-only data, the fact that they document establishment in dry locations does not necessarily imply that establishment in drier sites is common relative to wetter sites. Laboratory experiments have shown that

aspen seed germination is constrained by soil moisture, with seed germination reduced to 48% at substrate water potentials of -4.4 atm, and to 0% at -7.7 atm (McDonough, 1979). However, given that a single aspen tree can produce well over one million seeds in a given year (Maini and Cayford, 1968), even a very reduced fraction of germinating seeds (such as may occur in dry sites) might still allow for establishment. In areas and years of dry climate, the effect of climate may be partially offset by microsite factors that increase soil moisture such as topographic concavities (Williams and Johnston, 1984; Schott et al., 2014) and shading structures (Fairweather et al., 2014). Such features are common across post-disturbance landscapes, potentially expanding the range of inter-annual climatic conditions in which aspen can establish, survive, and grow (de Chantal and Granström, 2007; Landhäusser et al., 2010; Fairweather et al., 2014).

For all these reasons, it is likely that seedlings are theoretically able to establish across nearly all of aspen's western climate envelope, but with lower densities in drier areas, where seed germination or survival may be reduced (McDonough, 1979). Across our systematic sites, seedlings may have been present in dry areas, albeit at low densities that reduced the likelihood of occurrence in a plot. Additionally, reduced establishment in systematic sites with less average annual precipitation may partially be because these sites also tended to have increased post-fire shrub and herbaceous cover, which presumably created a more competitive environment with reduced survival (Le, 2017). Future studies which track seedlings through time across climatic gradients (similar to Chapter 3) will be important to determine whether patterns of decreased establishment in drier sites are indicative of similar negative impacts on growth and survival.

Though seedlings were more likely to establish in wetter sites, we found little

evidence that the years in which historical seedling establishment occurred were wetter or cooler than site averages. Instead, establishment was more likely to occur in years that were drier or hotter than average, even in sites with hot and dry average annual precipitation and temperature (Figure 5). In some sites, establishment occurred during periods of extreme drought (over two standard-deviations drier than average), contrary to the anecdotal hypothesis that seedling establishment only occurred during exceptionally favorable periods of climate. Since growth in aspen seedlings can be inhibited by interspecific competition (Le, 2017) and intraspecific competition with aspen suckers (Barnes, 1966), it is possible that in a given site, dry years may correspond with reduced competing vegetation, which would facilitate aspen seedling establishment. However, given that the majority of historical seedling establishment occurred after fires, another plausible explanation is that fires tend to burn in warm dry years and subsequent years may also be warm and dry (Brown, 2006). In other words, the years available for successful germination and early growth of seedlings may be more likely to be dry, on average, than a year at random. Additionally, seed availability may be higher during dry periods, since it is possible that smoke or drought-induced stress may stimulate trees to seed the following year (personal correspondence, K. Mock). However, factors controlling seed release in aspen are not well understood, and represent an area for future research (Landhäusser et al., 2019).

In systematic sites, aspen suckers had much higher modeled rates of occupancy than aspen seedlings, in sites with less average annual precipitation. Though suckers did experience slight declines in occupancy probability in drier sites, they may do better in these more arid sites than seedlings, which rely on moisture-dependent seed germination

and, at least initially, lack shared root reserves. However, over half of systematic sites with aspen seedling establishment contained no pre-fire aspen, representing an expansion of the area that aspen occupies in those fire footprints. In nine plots, seedlings were found at distances ≥1 km away from the nearest live aspen, allowing the species to occupy areas without pre-disturbance aspen populations. Dispersal distances of aspen seeds (10+ km; Landhäusser et al., 2010; Turner et al., 2003) are far greater than conifer seeds (generally within 200 m; McCaughey et al., 1981). As forest fires in the western U.S. are predicted to become larger (Schoennagel et al., 2017) and burn at higher severities (Abatzoglou et al., 2017), large high-severity fire patches will also become more common, with resulting increases in seed source distances (Donato et al., 2009). Research has largely focused on conifer regeneration, highlighting worries about declining post-fire conifer regeneration as result of both increasing seed source distances (Donato et al., 2009) and hotter, drier climate (Stevens-Rumann and Morgan, 2019). However, due to aspen's multiple regeneration mechanisms, post-fire aspen regeneration may help ameliorate declines in conifer regeneration. With suckering, aspen can regenerate following disturbance without the need of nearby seed sources. Through sexual regeneration, aspen seedling establishment is likely the most effective natural forest regeneration pathway in large treeless areas that were dominated by conifers pre-fire. A shift to increased aspen cover could still maintain many important ecosystem services; aspen have high levels of biodiversity (McCullough et al., 2013), increased soil carbon sequestration (Boča and Van Miegroet, 2017) and increased nutrient cycling (Légaré et al., 2005), relative to conifer forests.

Our systematic survey for seedling establishment occurred within areas that had

burned in 2018, in order to differentiate seedlings from suckers before growth had obscured morphological differences (Kreider et al., 2020). However, as a result, our systematic sites represent only a single year's cohort of post-fire regeneration, and this year may not be representative of general trends. Additionally, the sites do not span a large range of inter-annual climate variation. Climate in 2019—the year the majority of seedlings in systematic sites likely established—was cooler and wetter than average in nearly every fire area. It is possible that the ubiquity of seedling establishment across these fire areas is due, in part, to favorable climate. On the other hand, the analysis of establishment climate in historical sites showed that establishment is not restricted only to certain yearly climate conditions (e.g., wetter than average). Additional systematic surveys for aspen seedlings over multiple years would be valuable, in order to begin to examine the effect of inter-annual climate variation on seedling establishment rates at broad scales.

It is unclear why some seedling establishment occurs at low background levels (i.e., only a single seedling in a given area) while in other areas seedling establishment is widespread and prolific (e.g., in the 1988 Yellowstone, 2017 Brian Head, and 2018 Murdock fires). These differences may be tied to seed availability across time and space, an area that is not well understood. However, although densities of seedlings in the majority of systematic sites were low, even a single seedling can develop into a large clone, and low level rates of aspen seedling establishment might play an important role in maintaining or increasing genetic diversity in a population (Long and Mock, 2012). Ultimately, much is contingent on the subsequent survival of aspen seedlings. While several studies that tracked seedlings across multiple years report survival of a sizeable

portion through the period of observation (Romme et al., 2005; Fairweather et al., 2014), additional longer-term studies are needed to better understand the dynamics of seedling survival and, consequently, the role seedlings play in the eventual genetic composition of a mature stand. Genetic lines of evidence show that recent sexual regeneration is an important contributor of genetic diversity in aspen in the western U.S. (Mock et al., 2008), indicating that at least some seedlings survive and are recruited into mature aspen cohorts.

Overall, our results suggest that aspen seedling establishment may be quite common across climate and space. Though establishment may be reduced in drier sites within a fire footprint, we demonstrate that aspen seedlings have established across a wide range of climate variation, and were found in nearly every systematically surveyed fire in our study. Aspen seedling establishment may be a ubiquitous, if usually low-density, feature in post-disturbance areas, which create suitable microsites for seed germination and early growth. Sexual regeneration in aspen has received much less focus than asexual regeneration. Here, we present compelling evidence that seedling establishment is an important component of western aspen regeneration. Even in small numbers, aspen seedlings can play a disproportionately large role in the species' response to climate change. With the increased need for adaptive capacity and movement across the landscape, sexual regeneration in aspen will only become more important in an increasingly uncertain future. More broadly, aspen regeneration can help to offset reduced conifer regeneration and maintain forests in post-fire landscapes and the important ecosystem services they provide.

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CHAPTER 3

ASPEN SEEDLING ESTABLISHMENT, SURVIVAL, AND GROWTH FOLLOWING THE BRIAN HEAD FIRE[2]

Abstract

Quaking aspen (*Populus tremuloides*) is an important component of western U.S. forests, however knowledge concerning processes of aspen seedling establishment, survival, and growth are limited and frequently anecdotal. Seedling establishment in aspen may be increasingly important given changing climate and fire regimes and the increased need for regeneration which creates adaptive capacity and facilitates dispersal across the landscape. We explored patterns of aspen seedling establishment, and tracked survival and growth of 1,111 seedlings following a widespread post-fire establishment event in southern Utah. Seedlings occurred across large areas of the 29,000 ha fire footprint, with an average plot density of 19,807 seedlings ha^{-1}, and the probability of seedling establishment within plots positively related to elevation and negatively related to distance to seed source. Seedlings preferentially established in concave microsites and next to coarse woody debris. After two growing seasons, 37% of seedlings remained alive, with survival reduced by competition with suckers and other seedlings, and growth constrained by sucker competition.

Introduction

As fires in the western U.S. increase in size (Schoennagel et al., 2017), frequency

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(Westerling et al., 2006), and likely burn severity (Abatzoglou et al., 2017), there is concern about post-fire conversion into non-forested vegetation due to reduced tree regeneration in some areas (Stevens-Rumann and Morgan, 2019). Much of this loss in forest resilience is tied to regeneration failures, as seedlings establishing today face very different environmental conditions than those under which the previous forest established. Even in the absence of disturbance, changing environmental conditions can cause gradual changes in tree species composition, as species' ranges contract or expand to where conditions are more favorable for regeneration (Chen et al., 2011). However, fire can accelerate this process, rapidly altering tree species assemblages (Moser et al., 2010) or even catalyzing ecosystem state-shifts into shrub or grassland systems (Stevens-Rumann and Morgan, 2019). Additionally, increasingly large high-severity fire patches can reduce post-fire seed availability and increase seed source distances (Donato et al., 2009), further exacerbating tree regeneration failures and ecosystem shifts.

Research on post-fire regeneration in the western U.S. has largely focused on conifer species. However, quaking aspen (*Populus tremuloides*) is also an important component of western U.S. forests, where it is often the primary deciduous tree species, and contains high levels of understory and animal species diversity relative to conifer forests (Griffis-Kyle and Beier, 2003; Kuhn et al., 2011). Aspen is predicted to be negatively impacted by changing climate (Rehfeldt et al., 2009), necessitating an improved understanding of regeneration processes in aspen, especially in seed-based regeneration, which has received far less attention than asexual reproduction (Landhäusser et al., 2019). Seed-based reproduction in aspen may help ameliorate the predicted negative impacts of climate change on the species. Aspen's small, wind-dispersed seeds can travel

over 10 km (Turner et al., 2003), facilitating range shifts far more quickly than asexual resprouting. Reproduction from seed also increases genetic diversity, creating adaptive capacity with which to respond to changing future conditions (Mock et al., 2008).

Because aspen seedlings have only recently been acknowledged as an important regeneration pathway in aspen in the western U.S., knowledge concerning processes of aspen seedling establishment, survival, and growth are limited and frequently anecdotal (Landhäusser et al., 2019). However, some patterns are emerging. Seedling establishment appears to be highly confined to disturbed soils (Landhäusser et al., 2010; Romme et al., 1997), which allows aspen's small seeds to make contact with mineral soil and germinate. McDonough (1979) also demonstrated that germination of aspen seeds is dependent on adequate soil moisture, however it is unclear how frequently these requirements are met across time and space. Seedlings have been shown to preferentially establish next to logs (Fairweather et al., 2014) as well as in topographic concavities (Kay, 1993; Landhäusser et al., 2010), indicating that structures that increase soil moisture may be beneficial to seedling establishment, especially during years of drought (Fairweather et al., 2014).

While microsite requirements for seedling establishment are better characterized, patterns of landscape level occupancy are not well understood, since few studies have employed random or systematic sampling, instead choosing areas of highest seedling establishment densities (e.g., Kay, 1993). Seedling establishment is dependent on proximal mature aspen stands for seed dispersal (Gill et al., 2017; Turner et al., 2003), although likely to a lesser extent than conifer regeneration, due to increased seed dispersal distances. The effects of other landscape factors such as aspect, elevation, or slope are largely unknown.

Similarly, knowledge of factors impacting aspen seedling survival and growth are limited, because few studies reporting seedling establishment have tracked seedlings over time. Renkin et al. (1994) showed that survival in seedlings which established following the 1988 Yellowstone fires was negatively impacted by herbivory, flooding, leaf blight, and competition in areas of high density seedling establishment. Information on the effects of other factors on survival, and on seedling survival outside of the greater Yellowstone area, remain unexplored. Furthermore, few studies have tracked seedlings that established in areas with co-occurring aspen sucker regeneration, leaving an open question about how these two regeneration pathways interact to shape longer term stand dynamics.

We utilized a widespread post-fire aspen seedling establishment event and a network of randomly placed plots across gradients of fire severity and elevation to explore patterns of seedling establishment and success in the first two years after fire. Specifically, we asked: 1) Where do seedlings establish at both the landscape and microsite level, and what factors explain seedling abundance across the landscape? 2) Once established, what factors impact seedling survival and growth?

Methods

Study site

The Brian Head fire was started by human ignition on June 17, 2017 and burned 29,000 ha in southern Utah, in a mosaic of fire severity including large patches with no tree survival (Figure 7). The fire footprint spans over 1,200 m of elevation and a wide range of annual precipitation (400–1000 mm) and annual mean temperature (2.0–7.0° C) (PRISM Climate Group, 2018). Summer precipitation is monsoonal, with June generally

quite dry before summer rains occur in July and August. Pre-fire vegetation at lower elevations consisted largely of pinyon pine (*Pinus edulis*) and juniper (*Juniperus osteosperma* and *Juniperus scopulorum*) woodlands. Mid-elevation tree species included aspen (*Populus tremuloides*), ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), and white fir (*Abies concolor*), with aspen, subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and limber pine (*Pinus flexilis*) present at higher elevations. In June 2018, an usually large aspen seeding event occurred in and around the Brian Head fire area, and newly-germinated aspen seedlings were first observed in the fire footprint in September 2018.

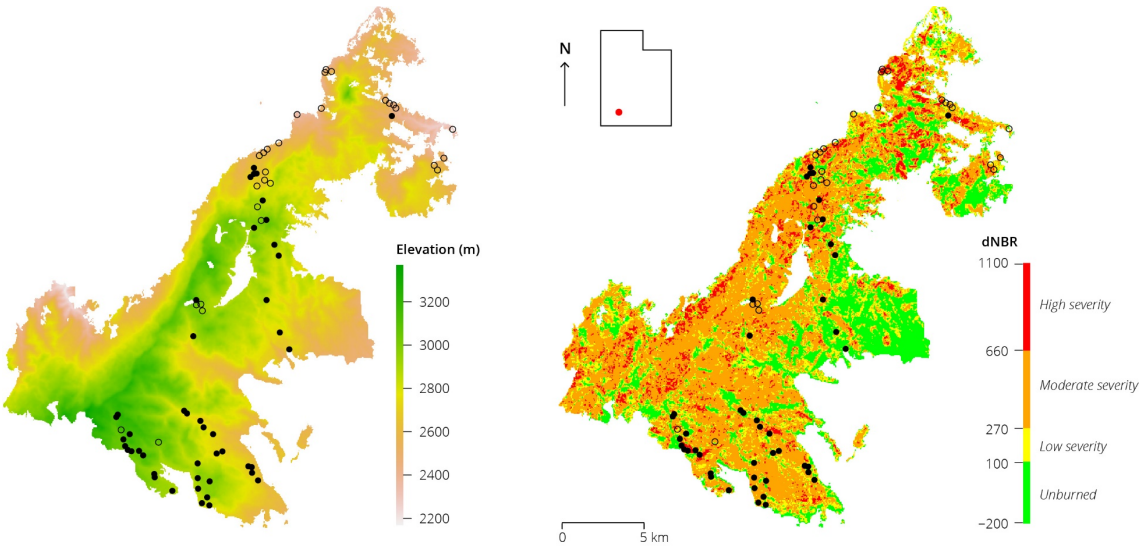

Figure 7: Elevation (*left*) and fire severity (*right*) of the Brian Head fire footprint. Plots with aspen seedling establishment are indicated by a filled circle; plots without seedling establishment by an open circle.

Plot establishment

We established 73 plots across the fire area in June 2018 (Figure 7) to quantify and monitor post-fire tree regeneration. Plots were located on Forest Service land in forested areas, and stratified by elevation and burn severity. Plots were randomly established between 50–400 m from a road, and at least 200 m from another plot.

Plot design and data collection

Each plot consisted of a 50 meter transect (parallel to contour lines) and a variable-width rectangular plot extending up to 10 meters upslope from the transect (modified from Stevens-Rumann et al., 2015). A width of 1–10 meters was chosen prior to sampling based on visual assessment of aspen seedling density within the plot and a goal of recording approximately 30 seedlings per plot. In the event that few or no seedlings were observed along the transect, the width was set to 10 m. Aspen seedlings were identified non-destructively using methods detailed by Kreider et al. (2020), which demonstrated 96% accuracy in testing in the Brian Head fire footprint. We permanently tagged all (or a random subset when densities were very high) aspen seedlings occurring within each plot in June 2019, soon after snow melted and plants had leafed out, measuring height and presence of herbivory. Following Landhäusser et al. (2010), we quantified the topographic position in which each seedling occurred. Topographic microsites within a 2.5 cm and 50 cm radius from the seedling were categorized as 1) level, 2) concave, or 3) sloped. Convex microsites were rare and were categorized as level. We recorded the presence of coarse woody debris (CWD) at two thresholds: 1) small CWD (2.5–10 cm in height) within 10 cm of each seedling and 2) large CWD (10+ cm in height) within 25 cm of each seedling. We categorized each seedling's distance to

the nearest aspen sucker, in five bins: 1) 0–15 cm, 2) 15–50 cm, 3) 50–100 cm, 4) 100–200 cm, and 5) 200+ cm. Finally, we recorded whether the seedling occurred on burned soil. We returned to all plots in September 2019, June 2020, and September 2020, to re-measure seedlings and record survival. Aspen seedling specimens from the Brian Head fire footprint be viewed at the Intermountain Herbarium at Utah State University or online at http://intermountainbiota.org (Catalog Nos. UTC00282407 and UTC00283351).

In the center of each plot, we recorded slope, aspect, and distance to the nearest live aspen tree of reproductive age. Along the transect, we measured herbaceous cover—including forbs, graminoids, and shrubs—in a 1 x 1 m quadrat every 10 meters. We measured density and height of post-fire establishing aspen sucker stems in 1 x 1 m quadrat every 5 meters. We also censused all overstory trees—dead and alive—over 8 cm diameter at breast height within a 200 m^2 circular subplot centered at 25 m along the transect to estimate the level of pre-fire aspen basal area. For a summary of all measured variables, see Table 5.

We calculated differenced Normalized Burn Ratio (dNBR) at each plot in Google Earth Engine (Gorelick et al., 2017) from Sentinel imagery (Parks et al., 2018). We obtained 30-year climate normals (1981–2010) of yearly precipitation and mean temperature for each plot from PRISM 800m datasets (PRISM Climate Group). Precipitation and temperature data were highly positively and negatively correlated, respectively, with elevation across sites. Because elevation data was resolved at a much finer spatial scale than climate variables (800 m pixels), we used only elevation in modeling, recognizing that it represents a proxy for the climatic gradient.

Table 5: Summary of potential model predictors. Mean and range are for un-scaled data. Plot-level predictors had a single value for each plot (all seedlings within the plot were assigned this value). Seedling-level predictors had observations made for each tagged seedling. "Tagged seedling mean" differs from "Plot mean" due to the fact that some plots had greater numbers of seedlings, skewing the "tagged seedling mean" towards the most conditions in which the most seedlings occurred. A predictor's inclusion in given model is indicated with an "X".

Predictor	Level	Description	Range	Plot mean	Tagged seedling mean	Occupancy model	Density model	Survival model	Growth model
Aspect	Plot	Sin-transformed folded aspect; 0 = NE, 2 = SW (measured using a compass at plot center)	0–2	1.14	1.33	X	X	X	X
Elevation	Plot	Height above sea level in meters (measured using GPS unit at plot center)	2782–3202 m	2782 m	2868 m	X	X	X	X
Slope	Plot	Slope in degrees (measured using a clinometer at plot center)	0–38°	14°	12°	X	X	X	X
dNBR	Plot	Differenced normalized burn ratio (scaled by 10^3; see Key and Benson (2006) for corresponding ordinal fire severity levels)	97–933	472	409	X	X	X	X
Seed-source distance	Plot	Distance from plot center to nearest live aspen tree of reproductive age	1–800 m	157 m	55 m	X	X		
Seedling density	Plot	Log_{10} transformed aspen seedling density within occupied plots	1.30–5.50 (untransformed: 20–318,000 stems ha^{-1})	3.33	3.91			X	X
Sucker density	Plot	Average number of sucker stems ha^{-1}	0–79,000 stems ha^{-1}	14,000 stems ha^{-1}	18,000 stems ha^{-1}	X	X	X	X
Herbaceous competition	Plot	Average percent cover of forbs, graminoids, and shrubs	0–28 %	7 %	7 %	X	X	X	X
Initial seedling height	Seedling	Height of tagged seedling in June 2019	0.5–9.0 cm	—	2.9 cm				X
Sucker distance	Seedling	Binned distance to nearest sucker	0–15 cm, 15–50 cm, 50–100 cm, 100–200 cm, 200+ cm (categorical)	—	200+ cm (mode)			X	X

Cluster	Seedling	Presence of another seedling within 10 cm	0 or 1 (binary)	—	0 (mode)	X	X
Large CWD	Seedling	Presence of coarse woody debris 10+ cm in height within 25 cm	Presence or absence (binary)	—	Absence (mode)	X	X
Small CWD	Seedling	Presence of coarse woody debris 2.5–10 cm in height within 10 cm	Presence or absence (binary)	—	Absence (mode)	X	X
Large topography	Seedling	Topographic microsite within a 50 cm radius from the seedling.	level, sloped, or concave (categorical)	—	Sloping (mode)	X	X
Small Topography	Seedling	Topographic microsites within a 2.5 cm radius from the seedling.	level, sloped, or concave (categorical)	—	Sloping (mode)	X	X

Analysis

We conducted all data-aggregation in the R statistical software (R Core Team, 2018), and used *tidyverse* packages (Wickham et al., 2019). We used a Bayesian framework to conduct the statistical analysis, including models of plot occupancy, seedling density, microsite preference, survival, and growth. For use in all models, continuous predictor variables (Table 5) were scaled and centered (mean of 0 and standard deviation of 1). We fit models using the *ulam* function in the *rethinking* package (McElreath, 2020) in R. This package interfaces with the *rstan* package to fit Stan models using Hamiltonian Monte Carlo (Stan Development Team, 2020). We ran each model with four chains of 4,000 samples, 1,000 of which were warmup. We verified model convergence using Gelman-Rubin convergence diagnostics (Gelman and Rubin, 1992) and by visually inspecting parameter trace plots.

Plot occupancy model

We modeled aspen seedling occupancy at the plot level using binomial logistic regression, with the following generalized linear model:

$$\text{seedling plot occupancy} \sim bernoulli(p)$$

$$\begin{aligned} logit(p) = \alpha + \beta_1 \times \text{dNBR} + \beta_2 \times \text{elevation} + \beta_3 \times \text{slope} + \beta_4 \times \text{aspect} \\ + \beta_5 \times \text{seed-source distance} + \beta_6 \times \text{sucker density} \\ + \beta_7 \times \text{herbacious competition} \end{aligned}$$

where p is probability of occupancy, α is the intercept term and β_x values are slope coefficients. We used uninformative priors, modeling $\alpha \sim normal(0, 1.5)$ and all slope parameters as $\beta \sim normal(0, 3)$. To compare aspen seedling and sucker occupancy, we

fit a model with plot sucker occupancy as the response variable, using the same structure and predictors as above, except for the removal of sucker density as a predictor.

Seedling density model

We modeled initial seedling establishment density of occupied plots using a linear model. Because seedling densities of occupied plots varied by several orders of magnitude, we used log-transformed density as the response variable.

$$\text{seedling density} \sim normal(mu, sigma)$$

$$mu = \alpha + \beta_1 \times \text{dNBR} + \beta_2 \times \text{elevation} + \beta_3 \times \text{slope} + \beta_4 \times \text{aspect} + \beta_5 \times \text{seed-source distance} + \beta_6 \times \text{sucker density} + \beta_7 \times \text{herbacious competition}$$

We used uninformative priors, modeling $sigma \sim exponential(0.5)$, $\alpha \sim normal(5, 3)$ and slope parameters as $\beta \sim normal(0, 3)$.

Microsite preference modeling

In order to model seedling preference for each categorical microsite variable (Small CWD, large CWD, small topography, large topography, sucker distance), for each variable we created two models; 1) modeling the probability that seedlings occurred in each category of the variable and 2) modeling the probability that systematically surveyed points in plots with seedling establishment occurred in each category (representing the "availability" of microsites, or expected probabilities of seedling establishment if it occurred randomly). We fit the following multinomial logistic regression models, using the "softmax" link function (McElreath, 2020), which extends the logistic function to multiple dimensions.

$$\text{seedling microsite} \sim multinomial(softmax[0, p_1, \dots, p_{n-1}])$$

$$\text{available microsite} \sim multinomial(softmax[0, p_1, \dots, p_{n-1}])$$

We used uninformative priors, modeling $p_1, \dots, p_{n-1} \sim normal(0, 5)$. The first level of a variable was set to be the reference level (represented by the 0 in the vector of inputs to the softmax link) and the remaining $n - 1$ levels were estimated. Although variables with only two levels (e.g., CWD presence variables) can be modeled using binomial instead of multinomial logistic regression, model predictions are identical since binomial regression is a special case of multinomial regression. In order to maintain consistency, we modeled binary variables within this multinomial framework as well. Changing the reference level yielded different parameter estimates, however the resulting model predictions remain the same. For this reason, we evaluated all models based on model-predicted probabilities, and transformed parameter posterior samples into a posterior of probability vectors using $softmax[0, p_1, \dots, p_n]$.

In order to derive a measure of preference, we calculated the percent difference from available conditions:

$$Preference = \frac{Modeled\ probability\ of\ seedling\ in\ microsite\ category - Modeled\ probability\ of\ microsite\ category\ availability}{Modeled\ probability\ of\ microsite\ category\ availability}$$

Preference values above zero indicate that seedlings established in that microsite category more often than expected; values below zero indicate establishment less often than expected.

Survival model

We modeled survival of individual tagged seedlings across the entire time frame using a binomial generalized linear model.

$$\text{seedling survival} \sim bernoulli(p)$$

$$\begin{aligned} logit(p) = {} & \beta_1 \times \text{dNBR} + \beta_2 \times \text{elevation} + \beta_3 \times \text{slope} + \beta_4 \times \text{aspect} \\ & + \beta_5 \times \text{sucker density} \\ & + \beta_6 \times \text{seedling density} + \beta_7 \times \text{sucker distance} + \beta_8 \\ & \times \text{herbacious competition} + \beta_9 \times \text{big topography} + \beta_{10} \\ & \times \text{small topography} + \beta_{11} \times \text{small CWD presence} + \beta_{12} \\ & \times \text{big CWD presence} + \beta_{13} \times \text{cluster} \end{aligned}$$

We used uninformative priors, modeling all slope/categorical parameters as $\beta \sim normal(0, 3)$. In addition to survival across the entire time frame, we fit three identical models to model survival in each time frame. For each model, data was subset to include only seedlings that were alive at the start of each timeframe.

Growth model

We modeled growth of tagged seedlings that were still alive at the end of the research study. We calculated growth as final height minus the initial height. We fit the following linear model, using the same predictors as in the survival model:

$$\text{seedling growth} \sim normal(mu, sigma)$$

$$\begin{aligned} mu = {} & \beta_1 \times \text{dNBR} + \beta_2 \times \text{elevation} + \beta_3 \times \text{slope} + \beta_4 \times \text{aspect} \\ & + \beta_5 \times \text{sucker density} \\ & + \beta_6 \times \text{seedling density} + \beta_7 \times \text{sucker distance} + \beta_8 \\ & \times \text{herbacious competition} + \beta_9 \times \text{big topography} + \beta_{10} \\ & \times \text{small topography} + \beta_{11} \times \text{small CWD presence} + \beta_{12} \\ & \times \text{big CWD presence} + \beta_{13} \times \text{cluster} + \beta_{14} \times \text{initial height} \end{aligned}$$

We used uninformative priors, modeling all slope/categorical parameters as $\beta \sim normal(0, 10)$ and $sigma \sim exponential(0.1)$.

Results

We observed aspen seedlings in 62% of plots (45/73) in June 2019. We permanently tagged a subset of seedlings in these occupied plots, for a total of 1,111 seedlings, and a mean of 26 seedlings per plot (median of 21). All 1,111 seedlings established on soil that had burned. Estimated establishment densities varied greatly among occupied plots, from 20–318,000 seedlings ha^{-1}. Mean establishment density in occupied plots was 33,012 seedlings ha^{-1} (median 2500 seedlings ha^{-1}) and 19,807 seedlings ha^{-1} across all plots (median 80 seedlings ha^{-1}). Over the course of the study, 136 (12.2%) tagged seedlings were removed from the dataset due to non-mortality causes, mostly from tags being chewed, pulled up, and carried away by animals, such that the fate of the original seedling was unknown. Of the remaining 975 tagged seedlings, 362 were still alive in September 2020, for an overall survival rate of 37.1% (Figure 8a). Survival rates varied by time window, with 74.0% survival during summer 2019, 56.2% during winter 2019–2020, and 82.5% during summer 2020. In two of the 45 occupied plots, all tagged seedlings had died by September 2020, however in both cases, surviving aspen seedlings were observed outside the plot nearby. Estimated mean density as of September 2020 of originally occupied plots dropped to 9635 seedlings ha^{-1} (median of 776 seedlings ha^{-1}) and across all plots, to 5781 seedlings ha^{-1} (median of 40 seedlings ha^{-1}). The percentage of tagged seedlings with visible herbivory increased over time, from no seedlings showing herbivory in June 2019 to 49% of seedlings in September 2020

(Figure 8b). Even with herbivory, mean height of tagged seedlings increased over time, from 2.9 cm in June 2019 to 18.8 cm in September 2020 (Figure 8c).

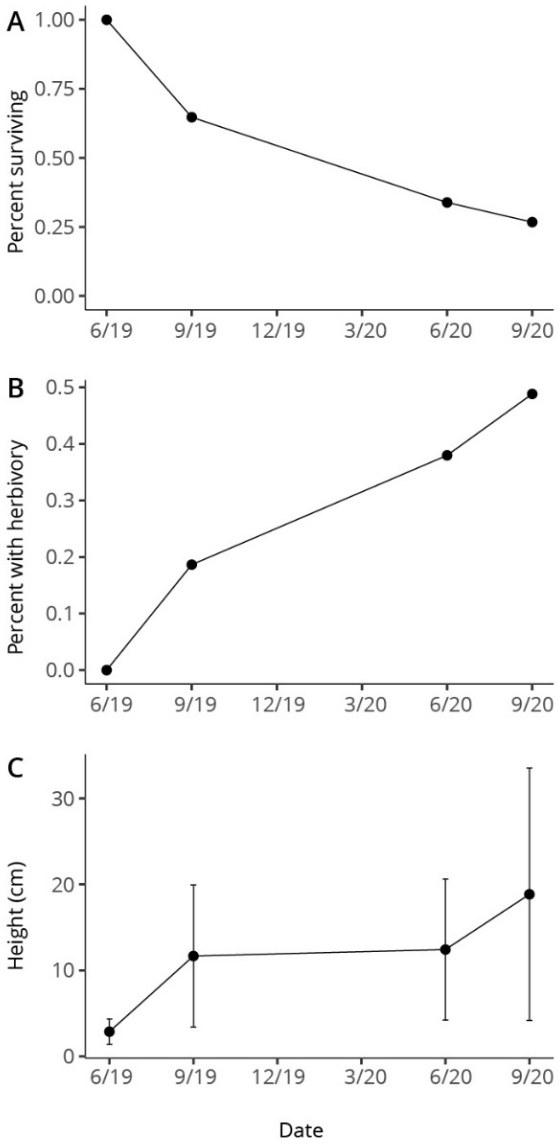

Figure 8: Seedling height, herbivory percentage, and cumulative survival across study timeframe.

Climate in the Brian Head fire footprint in 2018 (when seedlings established) was unusually hot and dry, with annual precipitation nearly a standard deviation lower than average, annual mean temperature nearly three standard deviations warmer than average, and summer (June–August) climate reflecting these trends. Summer climate was slightly hotter and drier than average in 2019, and nearly two standard deviations hotter and drier than average in 2020.

Patterns of seedling establishment

At the landscape level, higher seedling occupancy probabilities were associated with increasing elevation and shorter distances to seed sources (Figure 9). We did not find strong evidence that other variables, such as aspect, slope, herbaceous or sucker competition, or fire severity (CBI) influenced occupancy. Modeled seedling occupancy was slightly lower than sucker occupancy across much of the elevation range of the fire footprint (Figure 10). Modeled abundance of seedlings in plots was negatively associated with distance to seed-source. We did not find evidence that other predictors strongly influenced abundance (Appendix C).

Within plots at the microsite level, seedlings established more often than expected next to both small and large CWD. Seedlings also established more often than expected in both small and large concave topographic sites. Seedlings established less often than expected within 0–15 cm from a sucker, and more often than expected from 50–100 and 100–200 cm from a sucker (Figure 9).

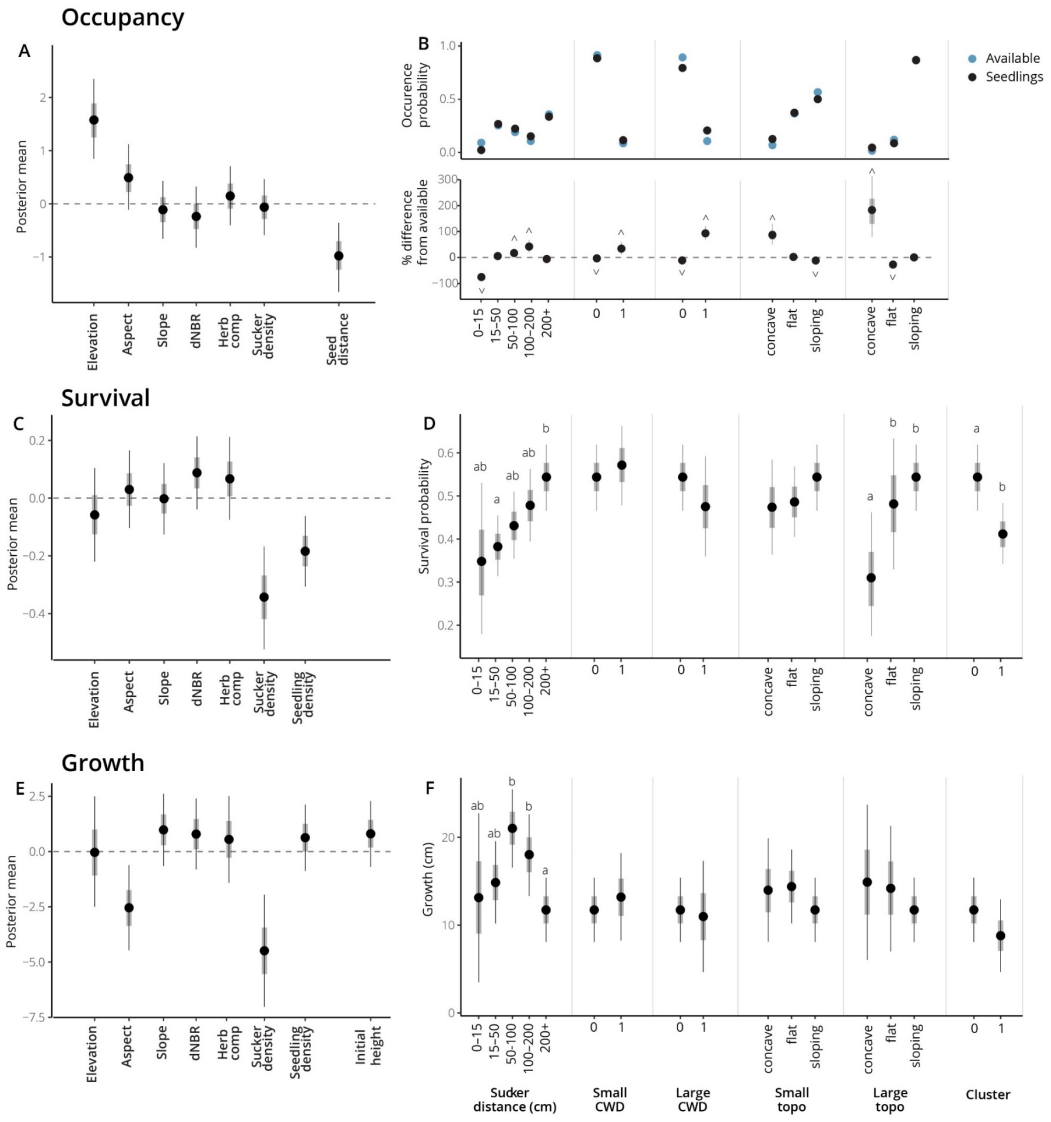

Figure 9: Occupancy, survival, and growth model results. Uncertainty in model posteriors or predictions are indicated by 89% (thin line) and 50% (thick line) compatibility intervals. A) Aspen seedling occupancy model parameter estimates. B) Top: Modeled occupancy probability of available (blue) and seedling (black) microsite locations. Bottom: Seedling preference for microsite categories (percent difference from available microsites). Compatibility intervals of most model estimates on the Top and Bottom are too small to see. C) Parameter estimates for continuous predictors in survival model. D) Model predictions for categorical predictors in survival model. Predictions for each variable were made with all other predictors at their means (if continuous) or modes (if categorical). Lowercase letters denote which categories have contrasts for which the posterior 89% compatibility interval does not overlap zero. E). Parameter estimates for continuous predictors in growth model. F). Model predictions for categorical predictors in growth model. Predictions for each variable were made with all other predictors at their means (if continuous) or modes (if categorical). Lowercase letters denote which categories have contrasts for which the posterior 89% compatibility interval does not overlap zero.

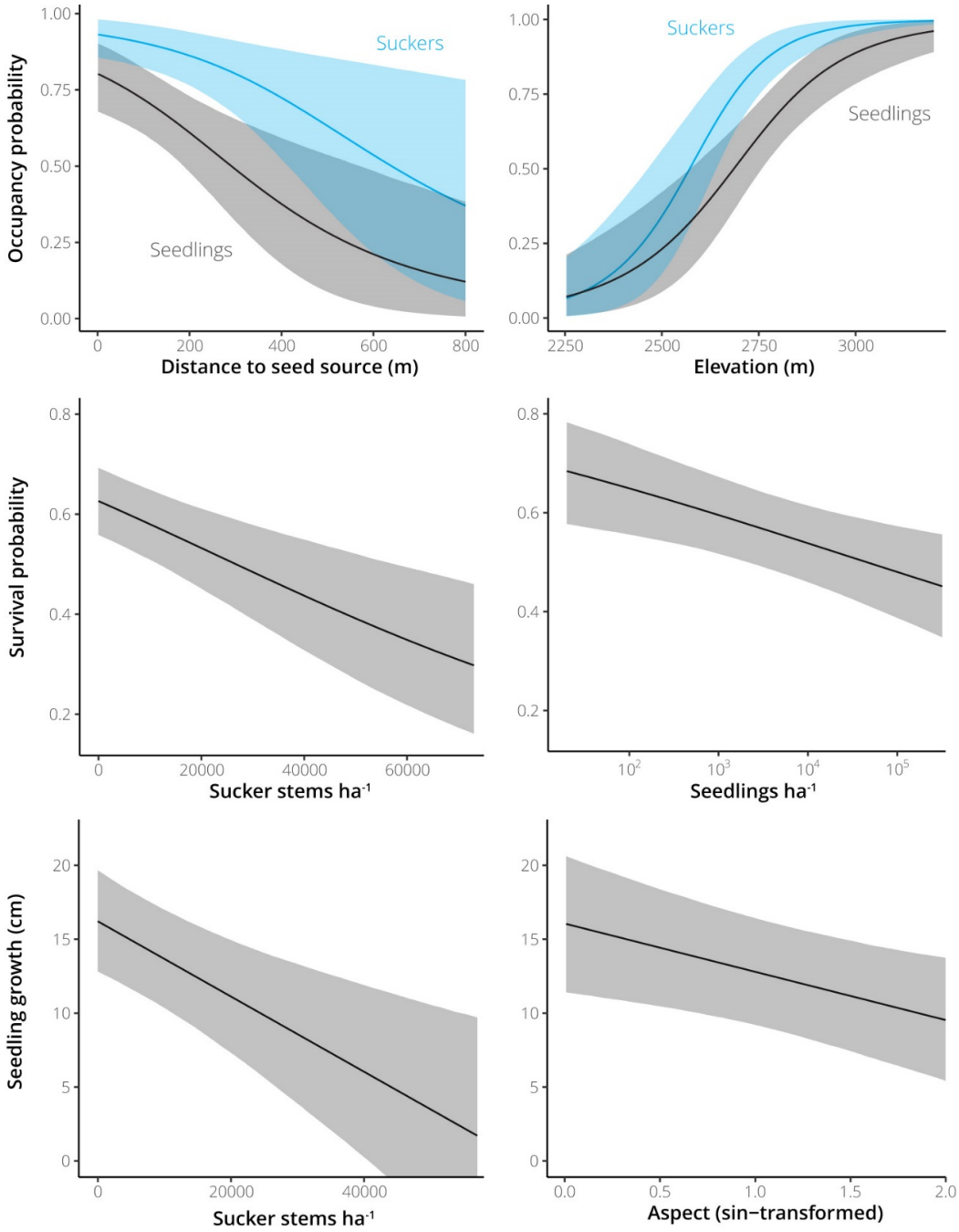

Figure 10: Modeled means of occupancy probability, survival, and growth. Predictions are shown as a function of selected continuous predictors (predictions shown for parameters for which posterior 89% compatibility intervals (Amrhein et al., 2019; McElreath, 2020) do not cross zero; this threshold is arbitrary and does not signify that other predictors have no effect on response variables). X-axes cover the minimum to maximum values of the input data, with predictions back-transformed to their raw (un-scaled) values for visualization. For each model prediction, other continuous and categorical predictors in the model have been held at their mean and mode, respectively. Uncertainty is shown with an 89% compatibility interval of the modeled means.

Patterns of seedling survival

Modeled seedling survival probability was reduced at higher plot seedling and sucker densities. Seedling survival was highest at distances further from the nearest sucker. Seedlings within 10 cm of another seedling (in a cluster) had lower survival than seedlings further than 10 cm from others. Seedlings in large concave topographic microsites had lower survival. We did not find evidence that small and large CWD or small topographic microsite strongly impacted survival (Figure 9).

Patterns of seedling growth

Seedling growth was most strongly impacted by plot sucker density, with decreased growth in plots with more sucker stems. Growth was also lower at aspects closer to SW, and higher closer to NE aspects. We did not find strong evidence that CWD presence, topographic microsite category, or cluster strongly impacted growth (Figure 9). There was a trend toward increased growth as the distance from a seedling increased from 0–15 cm to 50–200 cm. Tables of parameter and contrast posterior estimates for all models can be found in Appendix C.

Discussion

The seedling establishment that we documented across the Brian Head fire footprint is one of the largest, most widespread events of aspen seedling establishment identified in the western United States, and the first study to track survival and growth of seedlings across wide elevation and climate gradients. Seedlings were common across large swaths of the 29,000 ha fire footprint, from high elevation sites with cooler, wetter climate to low elevation sites at the edge of aspen's distribution. While suckers were

present in slightly more plots than seedlings (and generally in higher densities), modeled occupancy rates were largely comparable across elevation, indicating that seedlings and suckers were occupying similar niches across the landscape.

Compared to conifer seedlings, aspen seedlings were orders of magnitude more common; in 36,500 m^2 of searched area, we initially found only 11 post-fire conifer seedlings in 2018, and after two additional summers of measuring mortality and establishment in September 2020, there were only 19 living conifer seedlings across the entire searched area. Compared to the estimated nearly 75,000 aspen seedlings in the same amount of search area in June 2019 (estimated 22,000 as of September 2020), aspen seedlings represent the only significant sexual regeneration that has occurred, three years following the fire. It is important to note that aspen is an early successional species, and some conifer species may not establish on equivalent time scales. However, a lack of conifer regeneration following fires has been increasingly noted in other areas of western conifer forests (Stevens-Rumann and Morgan, 2019). Given the longer dispersal distances of aspen seeds and their ability to immediately take advantage of post-disturbance conditions, sexual regeneration in aspen may represent an important avenue for maintaining forests on the landscape (Chapter 2), especially in fires with large patches of high burn severity. Additionally, the increasing amount of area burned in the western U.S. (Westerling et al., 2006) might present a corresponding increase in the opportunity for aspen regeneration by seed, given how tightly seedling establishment is linked to bare mineral soil.

Establishment patterns of aspen seedlings following the Brian Head fire are largely consistent with other similar studies. We did not observe any aspen seedling

establishment occurring on soil that did not burn, adding weight to our understanding that seeds are highly dependent on disturbed soil to germinate and survive. However, plot differenced normalized burn ratio (dNBR) did not explain variance in seedling occupancy, likely because all our plots had burned to varying degrees, and thus all contained at least some suitable soil for seedling establishment. We also found, as expected, that seedling establishment was proximity to seed sources, in keeping with the handful of studies that have surveyed aspen seedlings across a landscape (e.g., Gill et al., 2017; Turner et al., 2003). However, compared to conifer regeneration, aspens were much less dependent on nearby seed sources, with establishment occurring in excess of 600 m away from potential seed sources in several plots. Seedlings established with much higher probability at higher elevations within the fire footprint, possibly as a result of increased seed availability due to more ubiquitous aspen distribution at higher elevations, or because increased precipitation in these higher elevation sites was more conducive to seed germination (McDonough, 1979). Because seedlings were not witnessed until September 2018, at least nine months of mortality potentially occurred prior to tagging and monitoring of seedling establishment in June 2019. Modeled occupancy may thus incorporate some influence of mortality.

The average density of seedlings across the landscape was lower than some documented occurrences such as those in Yellowstone National Park (Kay, 1993). However, many of these historical occurrences were not randomly sampled, and researchers instead chose areas of highest seedling density. We observed areas in the Brian Head fire footprint in June 2019, outside of sampled plots, with over 300 seedlings occurring per m^2. This would scale to over three million seedlings ha^{-1}, on a similar order

of magnitude with the highest Yellowstone estimates (11.5 million seedlings ha^{-1} based on one transect; Kay, 1993).

Similar to Romme et al. (1997), we did not find very strong predictors of seedling abundance. Contrasting the results of that study, we did not find an association between fire severity and abundance; instead, seedling abundance in the Brian Head fire footprint seems to be negatively (albeit weakly) linked to seed source distance. However, abundance varied by many orders of magnitude even in sites close to live aspen, and is likely controlled by other factors we did not measure such as seed fall intensity. Distance to seed source is likely a weak proxy for actual propagule pressure, explaining the statistical link between seed-source distance and seedling abundance. Little is known about what controls timing, amount, and spatial distribution of seed fall in aspen, representing an important area of future research (Landhäusser et al., 2019).

Similar to findings by Fairweather et al. (2014) and Landhausser et al. (2010), seedlings showed preferential establishment next to CWD and in concave microsites. Establishment climate of in 2018 was unusually hot and dry, and could have led to increased establishment in these microsites, which likely increased shade and soil moisture retention (Fairweather et al., 2014). Though seedlings were more likely than expected to establish in concavities and next to CWD, we found no evidence that these structures facilitated seedling success (aside from any higher survival that may have occurred, unobserved, in these microsites prior to June 2019). Seedling survival and growth over the course of the study was largely equivalent between presence or absence of CWD and topographic microsites. Though such microsites may increase soil moisture, they also tended to have higher seedling densities, and the high level of competition may

be the driving force behind equivalent or increased mortality in these locations. It is also possible that seedlings established preferentially next to logs and in concave microsites not because these conditions were more conducive to germination, survival, and growth, but rather because logs and depressions better trapped aspen's cottony pappus as it moved across the landscape.

While we reported relatively high rates of mortality compared to other studies (e.g., Fairweather et al., 2014; Romme et al., 2005), we also tracked survival during an earlier life-stage than many studies, when densities were still much higher. Given that initial seedlings densities can be as much as several hundred per square meter, high initial mortality is not surprising, and likely slows as surviving seedlings become more resilient several years following establishment (Fairweather et al., 2014; Romme et al., 2005). The overabundance of unique genetic individuals in this initial period also provides an opportunity for adaptive evolution (Mock et al., 2008). Indeed, competition appears to be a driving force of seedling mortality in the early years post-establishment, mirroring findings from other studies (Renkin et al., 1994). Survival was constrained by intraspecific competition with other seedlings as well as surrounding suckers, as quantified in multiple ways (e.g., plot-level densities as well as physical proximity to a sucker or nearby seedling).

Though suckers may outcompete seedlings where they co-occur due to shared resources and increased initial growth of suckers, seedlings established in many areas with few or no suckers present, and may do best in these conditions. Given the great dispersal distance of aspen seed, it is presumable that in many footprints with aspen seed release, the extent of propagule pressure is greater than the area in which aspen occurred

pre-fire. Aspen seed would then fall in both areas of pre-fire aspen where suckering is more abundant, as well as in gaps between clones where suckering is absent. In this way suckers and seedlings may represent two parts of a complementary regeneration strategy: suckers can regenerate existing areas of aspen—likely out-competing seedlings—when that clone is well-adapted to site conditions; and seedlings can expand aspen cover into new areas or compensate when sucker regeneration is low.

We did not find strong evidence that competition with herbaceous vegetation reduced seedling success, perhaps because vegetative cover other than aspen suckers was not pervasive across many sites. However, it is likely that increased herbaceous vegetation would negatively seedling success in similar ways to sucker cover, due to more competition for resources such as water and light.

After two full growing seasons, average height of seedlings was still relatively low, well below ungulate browse height and much less than co-occurring suckers, which had achieved heights over two meters in many places. However, browsing did not appear to be a significant source of mortality in seedlings; in most cases herbivory was minor, confined to several leaves removed. Herbivory may be less of a concern in the Brian Head fire footprint compared to other studies (e.g., seedling regeneration in Yellowstone National Park) due to the sheer amount of regenerating aspen suckers and seedlings over a large fire area that collectively reduce herbivory pressures (Wan et al., 2014). Modeled seedling growth was lower in plots with southwesterly aspects, potentially due to decreased soil water retention and storage (Geroy et al., 2011). However, modeled occupancy gave some evidence for the opposite trend, suggesting that different mechanisms may control occupancy relative to subsequent growth. Similar to survival,

growth of surviving seedlings was negatively related to increased sucker competition. Highest growth occurred in seedlings that were at 50–200 cm away from the nearest sucker. While the model suggested that seedlings greater than 200 cm from a sucker had decreased growth, this may be influenced by plots which had no suckers present, but in which seedling growth was decreased for other reasons (such at the lower edge of aspen's distribution with decreased soil moisture).

Though our study adds to a broader understanding of aspen seedling establishment and early success, the timeframe is nonetheless quite short, and may not be indicative of long-term patterns. Though other studies do report relatively high continued survival of seedlings (e.g., Fairweather et al., 2014; Romme et al., 2005), suggesting that they are not merely a transient occurrence, we plan to continue to monitor the sites presented here. Continuing to track long-term survival and exploring the impact of intraspecific competition with suckers and seedlings will tell us more about the role that aspen seedlings play in post-fire succession. It is also important to better understand drivers of aspen seed availability across time and space. Aspen seedling establishment is an underexplored part of western aspen seedling ecology, and may be increasingly important given changing climate and the increased need for regeneration methods which create adaptive capacity and facilitate movement across the landscape.

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CHAPTER 4

METHODS FOR DISTINGUISHING ASPEN SEEDLINGS FROM SUCKERS IN THE FIELD[3]

Abstract

Quaking aspen is a common component of post-disturbance landscapes, in part due to its ability to regenerate via asexual suckers. Previously viewed as exceedingly rare in the western United States, sexual seedling establishment is increasingly seen as another important natural regeneration pathway for aspen, because sexual regeneration increases genetic diversity and facilitates long-distance dispersal. However, aspen seedling research is hampered by difficulties in visually distinguishing seedlings from suckers in the field, and few resources exist to guide managers and researchers. We present methods for distinguishing aspen seedlings from aspen suckers, suitable for use in field studies. Using these methods, we achieved 99% predictive accuracy in a recently-burned area in southern Utah, though accuracy decreased to 90% following one summer's growth, as seedlings and suckers became more similar in appearance.

Introduction

Monitoring regeneration of post-disturbance vegetation is a frequent goal of managers and researchers. As the most widely dispersed tree species in North America (Little, 1971), quaking aspen (*Populus tremuloides*; hereafter "aspen") regeneration is a

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[3] Kreider, Mark R., Larissa L. Yocom, and Karen E. Mock. 2020. "Methods for Distinguishing Aspen Seedlings from Suckers in the Field." *Journal of Forestry* 118 (6): 561-568. Reproduced by permission of Oxford University Press.

component of many post-disturbance areas, especially in the western United States, where it is frequently the primary deciduous forest tree species. As a clonal species, aspen regenerates in two ways; originally establishing through a sexual seedling, and thereafter by asexual suckers, as an individual clone expands. While suckers are routinely monitored, observation and monitoring of aspen seedlings is hampered by difficulties in accurate seedling identification. As an early paper on aspen management stated, "It is often exceedingly difficult to distinguish with certainty between seedlings and sprouts [suckers]… [since they are] practically identical in appearance…. The distinction rapidly increases in difficulty with the age of the tree…. Just what the proportion of suckers to seedlings is remains an unsolved problem" (Weigle and Frothingham, 1911, p. 21).

Aspen seedling regeneration was historically ignored in the western United States, because seedlings were thought to be unable to establish in hotter, drier climates (Long and Mock, 2012; McDonough, 1979). In recent years, genetic work (Mock et al., 2008) and a number of confirmed instances of seedling establishment (e.g., Williams and Johnston, 1984; Kay, 1993; Renkin, Despain, and Clark, 1994; Romme et al., 1997; Quinn and Wu, 2001; Fairweather, Rokala, and Mock, 2014; Krasnow and Stephens, 2015; Gill et al., 2017) have contributed to the growing consensus that sexual reproduction is an important component of aspen ecology (Long and Mock, 2012). Aspen seedlings are of particular research interest because unlike suckers, seedlings enable adaptation to climate change through increased genetic diversity and by facilitating migration with long-distance seed dispersal (Landhäusser et al., 2019).

Though aspen seedlings are increasingly seen as ecologically significant, few resources exist to guide managers and scientists interested in identifying and monitoring

seedlings in natural settings. This is compounded by a short window of feasible differentiation, after which seedlings themselves begin to sucker. Thus, the vast majority of studies exploring post-fire aspen regeneration either assume that regeneration is exclusively asexual (e.g., McIlroy and Shinneman, 2020) or the possibility of sexual regeneration is never mentioned (e.g., Pelz and Smith, 2018; Rhodes et al., 2018). Here we present a framework for identifying young aspen seedlings, to help managers and researchers explore the important role seedlings play in aspen regeneration, ecology, and adaptive evolution.

Though young aspen stems can be excavated to definitively tell whether they are a seedling or sucker, we present non-destructive methods suitable for use in studies that monitor the growth and survival of aspen seedlings through time. These methods were developed to distinguish naturally-occurring aspen seedlings from suckers in permanent plots across the 2017 Brian Head fire area in southern Utah. Widespread aspen suckering occurred following the fire in 2017, as well as in 2018 and 2019. In July 2018, unusually heavy aspen seed release was noted independently in several locations near Brian Head by landowners, land managers, and researchers. Newly germinated seedlings, many with cotyledons still attached, were observed across much of the fire footprint in early September 2018 (Figure 11). Seedlings were identified using the methods described below in the summer of 2019. Though our particular case study is post-fire, sexual aspen regeneration can occur after other types of disturbance (Faust, 1936; Landhäusser et al., 2010; Williams and Johnston, 1984), and our methods remain applicable in these instances.

Methods for Distinguishing

The following methods were developed through observation of seedlings and suckers across the Brian Head fire area, and through integration of findings from other studies that report identifying characteristics of aspen seedlings (e.g., Kay, 1993; Renkin, Despain, and Clark, 1994; Krasnow and Stephens, 2015). Morphology of seedlings is diverse, and no single attribute is likely to be universally predictive alone. However,

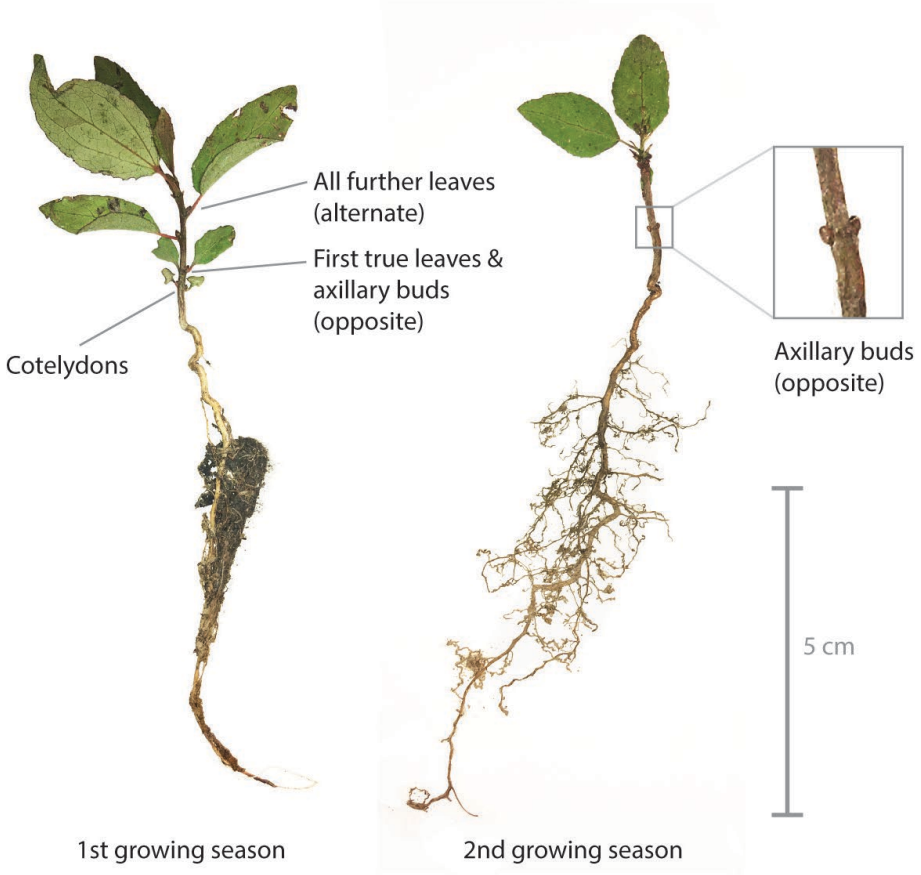

Figure 11: *Left:* A seedling from the Brian Head fire area in its first growing season (2018). Cotyledons may still be visible, and the first true leaves are opposite and originate directly above the cotyledons. All further leaves are alternate. *Right:* A seedling from the Brian Head fire area in its second growing season (2019). Axillary bud scars from the first true leaves may still be visible in subsequent growing seasons. These and other aspen seedlings can be viewed at the Intermountain Herbarium at Utah State University or online at http://intermountainbiota.org (Catalog Nos. UTC00282407 and UTC00283351).

when used as an ensemble, we found this suite of attributes useful in differentiation.

Cotyledons and leaf arrangement

If sampled in the first growing season, paired cotyledons are an indication of seedling origin (Figure 11). As noted by Renkin, Despain, and Clark, (1994), seedlings can also be identified by the first pair of true leaves (and axillary buds) which are nearly opposite and originate immediately above the cotyledons (Figure 11). Subsequent leaves are alternate, like all those of suckers (Renkin et al., 1994) and adult aspen (Little, 1980). Similar to Renkin, Despain, and Clark, (1994), we note that the axillary bud scars from this first pair of true leaves may still be visible in the second growing season (Figure 11). While the presence of cotyledon and/or opposite axillary bud scars is a strong identifying characteristic, its absence does not necessarily imply sucker origin. Bud scars can be obscured by continued growth, covered by the soil level, or altogether lost through herbivory.

Figure 12: Young aspen seedlings (left) tend to have distinct leaf morphology from aspen suckers (right). Photos by M. Kreider.

Leaf shape and size

In the initial growing seasons, the leaves of young seedlings are narrower and more lanceolate than the familiar cordate, or heart-shaped, form of sucker and mature aspen leaves (Figure 12; Renkin, Despain, and Clark, 1994). We also found sucker leaves to be larger, on average, than those of aspen seedlings. Morphological differences persist at least through the second growing season (Renkin et al., 1994), but disappear shortly thereafter as seedlings and suckers become virtually indistinguishable (Kay, 1993).

Height differences

Root suckering is generally robust following fire, with suckers often able to resprout later the same season (personal observation, K. Mock). On the contrary, seedlings may not establish until the subsequent year, if the timing of seed release does not align with the post-fire period. Furthermore, without an extensive root system, seedlings initially grow much more slowly than suckers (Krasnow and Stephens, 2015). Together, these differences create a one to two-year window after seedling establishment in which seedling and sucker cohorts are noticeably different in mean height and seedlings are more easily observed (Figure 13). Beyond this time period, seedling and sucker height distributions increasingly overlap and height is no longer a useful identifying characteristic (Figure 14).

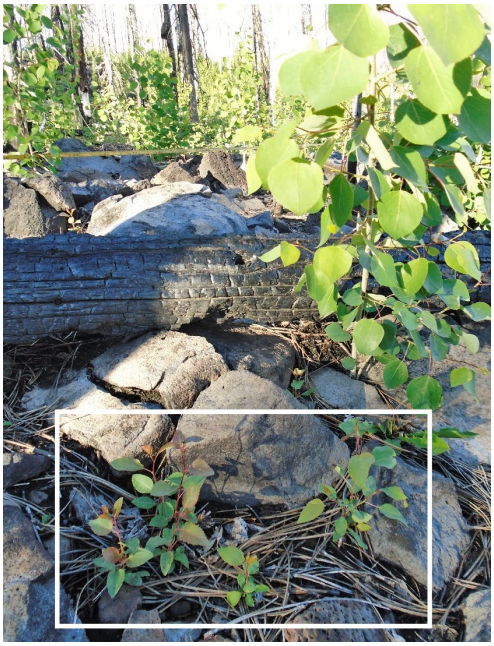

Figure 13: Aspen seedlings (in white box) are much shorter than suckers (top half) for the first several years following a fire. Photo by M. Kreider.

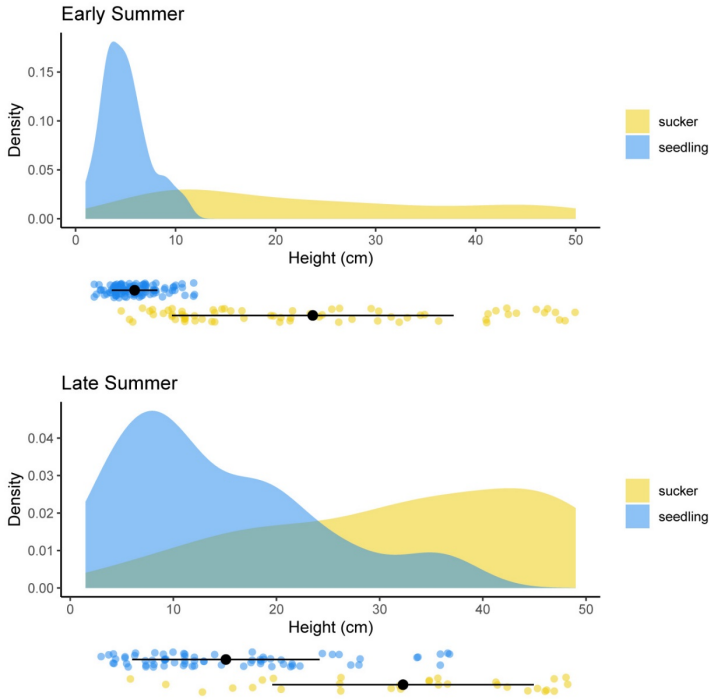

Figure 14: Kernel density estimates of seedling and sucker heights at the beginning of the second growing season (2019; "Early Summer") and at the end of the same season ("Late Summer"). Individual heights of seedlings and suckers are also displayed, along with mean height (black point) and one standard deviation above and below (black line).

Stem differences

We observed that seedlings have much thinner stems, on average, than suckers, at least through the seedlings' second growing season (Figure 15). This is likely due to initial differences in growth rates between seedlings and suckers, since suckers arise from existing roots and thus receive more resources at the outset. Stem differences can be used to distinguish seedlings in their second year of growth from newly sprouted suckers of similar height, as these new suckers have green stems that are not yet woody (Figure 15).

Figure 15: Seedling (*left*) stems tended to be thinner than sucker (*right*) stems at equivalent heights. Though suckers continue to send up additional shoots which are of similar height to already established seedlings, the entirety of these new suckers stems are new, green non-woody growth (*right*), as opposed to older seedlings which have a portion of woody prior growth (*left*). Photo by M. Kreider.

Microsites

Seedlings generally establish on bare mineral soil (Einsphar and Winton, 1976; Landhäusser et al., 2010). While not universal, we found many seedlings clustered in sheltered microsites such as depressions and along logs (Figure 16). Other studies have reported similar findings (e.g., Landhäusser, Deshaies, and Lieffers 2010; Fairweather, Rokala, and Mock, 2014; Schott, Karst, and Landhäusser, 2014; Krasnow and Stephens, 2015), indicating that these areas may be useful initial starting locations when searching for aspen seedlings in a post-disturbance environment. This pattern is likely due to a combination of soil moisture retention and deposition patterns of the cottony pappus associated with seeds.

Figure 16: Seedlings growing next to a log. Photo by M. Kreider.

Proximity to pre-fire aspen

Suckers must sprout from existing root systems and are therefore dependent on nearby pre-fire aspen. If it is known with certainty that no aspen existed in the vicinity prior to the fire, then any establishing aspen individuals are likely to be seedlings. However, it can be difficult to reliably confirm that aspen were not present, as fires can obscure or consume evidence of pre-disturbance vegetation. Additionally, lateral roots can extend more than 30 meters from mature aboveground trees (Buell and Buell, 1959). Thus, this method is only reliable at distances well beyond that (e.g., > 100 m) where it is known with certainty that no pre-fire root systems exist in the area.

Assessment of Predictive Accuracy

Using destructive sampling, we assessed our ability to non-destructively identify aspen individuals as seedlings or suckers. In June of 2019, we located two high severity burned areas within the Brian Head fire footprint where 1-year old seedlings and 1- and 2-year old suckers were both abundant. The two sites were approximately 2 km apart. At each site, we established a 50 m x 2 m belt transect. Within each transect, all aspen individuals less than or equal to 50 cm in height were predicted to be either a sucker or a seedling using the identification methods described above. This height cutoff was chosen because extensive opportunistic sampling by root excavation across the Brian Head fire footprint failed to identify any seedlings above approximately 20 cm in height; individuals above 50 cm were thus known with near certainty to be suckers. After height measurement and nondestructive prediction, each individual was carefully excavated using a garden trowel to determine its identity. Suckers were identified by the presence of a taproot that connected to larger lateral roots, while seedlings were identified by the

presence of filamentous, branching roots which each tapered to a terminus without connecting to any other roots. We returned to both sites in September 2019 and repeated the predictive accuracy assessment on a new transect adjacent to the first, to test whether accuracy decreased following summer growth. In one of the sites on this return visit, a 30 m x 2 m transect was used instead due to spatial constraints; all other methods were implemented identically.

Results

We systematically predicted and excavated 276 aspen individuals overall, 99 of which were suckers and 177 seedlings (Table 6). Distributions of seedling and sucker heights are displayed in Figure 4. Average height of seedlings in the early summer (n = 107) was 5.0 cm (SD = 2.3 cm) and 14.3 cm (SD = 9.6 cm) in the late summer (n = 70). Average height of suckers (bounded <50 cm) in the early summer (n = 69) was 23.2 cm (SD = 14.4 cm) and 32.4 cm (SD = 13.3) in the later summer (n = 30). With a total sampled area of 360 m^2, densities were 0.49/m^2 for seedlings and 0.28/m^2 for suckers 50 cm or less in height. Individuals were predicted correctly in 265 cases (96%) overall. However, predictive accuracy was lower by late summer, with 91 of 100 (91%) individuals predicted correctly compared to 174 of 176 (99%) in the early summer assessment. Overall, suckers were misidentified as seedlings slightly more often than seedlings were misidentified as suckers.

Table 6: Contingency table of predictive accuracy for aspen individuals under 50 cm by time and true status. Early summer assessment occurred June 19–23, 2019 while Late Summer assessment occurred September 14-15, 2019.

	Early summer	**Late summer**	**Total**
Seedling	107 / 107 (100%)	65 / 70 (92.9%)	172 / 177 (97.2%)
Sucker	67 / 69 (97.1%)	26 / 30 (86.7%)	93 / 99 (93.9%)
Total	174 / 176 (98.9%)	91 / 100 (91.0%)	265 / 276 (96.0%)

Discussion

Our identification methods had a high level of predictive accuracy, suitable for monitoring applications. The predictive accuracy assessment revealed a slight error bias between seedlings and suckers, with suckers more likely to be misidentified as seedlings than vice versa. However, we conducted our predictive accuracy assessment in areas of high-density co-occurring seedlings and suckers in order to subject our methods to the most difficult conditions. Identification would be less difficult in areas where no pre-fire aspen occurred in the vicinity before fire, for example. Thus, we believe that our accuracy assessment is a conservative estimate, compared to accuracy rates if applied across an entire fire footprint.

We believe that these methods are widely applicable for aspen seedlings across the western United States. The methods are based not only on our observations of seedlings in the Brian Head fire area, but also on observations from across the western United States (e.g., Kay, 1993; Renkin, Despain, and Clark, 1994; Krasnow and Stephens, 2015), which all describe aspen seedling and sucker morphological differences in agreement with our own observations. Though we tested predictive accuracy of these methods only within a single fire footprint, the characteristics observed are unlikely to be

due to a restricted genotype because aspen are open pollinated, with both pollen and seeds dispersed widely (McDonough, 1985; Turner et al., 2003), and many different clones in the Brian Head fire area were seeding in 2019 (Personal observation, K. Mock). Furthermore, within permanent plots across the fire area, morphological differences between seedlings and suckers remained consistent over a variety of aspects and nearly 1000 meters of elevation difference, suggesting that these methods are robust to a wide range of landscape conditions.

The predictive accuracy assessment took place in the second growing season after seedling germination was observed, two years following fire. While we demonstrated high levels of seedling identification accuracy during this early time window, as seedlings begin to resemble suckers in morphology, and height differences were not as pronounced, accuracy decreased. We predict that by the third growing season of seedlings, height differences will cease to be a useful differentiating characteristic and that visual identification by any means may become impossible soon afterward (Weigle and Frothingham, 1911). Following this, the only way to differentiate seedlings from asexual regeneration is through costly genetic methods, a technique that is not feasible across large areas of a fire area. Discernment is further complicated because seedlings can form their own asexual suckers even as soon as the first full growing season following germination. For all these reasons, it is vital that seedlings be identified as soon after they have germinated as possible, preferably within the first two growing seasons. Once identified, a subsample can be tagged and followed to track growth, survival rates, and landscape patterns of clonal recruitment.

Finally, it is important that in new sites these prediction methods should first be

validated for a subset of seedlings/suckers using excavation. We also recommend that caution be used when only a single seedling is observed in a plot, since seedlings are frequently clustered and unlikely to occur without nearby seedling observations.

The methods presented here offer scientists and managers a guide for differentiating aspen seedlings from their asexual counterparts following disturbance. Aspen seedlings may play an important role in the species' response to climate change through increased genetic diversity and dispersal potential. Increased genetic diversity may also facilitate adaptation to other selection pressures, such as ungulate and insect herbivory (Barker et al., 2019; Lindroth and St. Clair, 2013) and drought conditions (Griffin et al., 1991; Li et al., 2010). For these reasons, it is important to effectively identify, protect, and monitor seedling populations and the genetic and phenotypic diversity they contain. Effective identification of aspen seedlings is the first step toward addressing the many knowledge gaps remaining in aspen seedling ecology (Landhäusser et al., 2019). We hope that these methods will facilitate aspen seedling research and reduce barriers that have previously hampered observation.

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CHAPTER 5

CONCLUSION

This thesis adds to the growing consensus that aspen seedling establishment is a much more common occurrence than once believed. Historical occurrences of seedling establishment have been documented in geographic areas spanning much of the western U.S., from the northern Rocky Mountains to areas near the Mexican border, where aspen occurs in isolated pockets. The systematic survey of fires that burned in 2018 showed that nearly every fire footprint we searched contained at least low levels of seedling establishment. Aspen seedling establishment may be a ubiquitous, if generally low-density, feature in post-disturbance areas, which create suitable microsites for seed germination and early growth.

Climate of sites with documented seedling establishment in the western U.S. spans a wide range of average annual temperature and precipitation. Though redemonstrate a potential average annual precipitation threshold of 500 mm, seedlings have been documented across the majority of aspen's western U.S. climate envelope. Contrary to historical assumptions, we show that in occurrences in the literature, establishment has actually occurred more often during drier and hotter years than average. In some sites, establishment occurred during periods of extreme drought, indicating that seedlings are not as constrained by arid conditions as once thought. Seedlings have likely occurred across space and time in the past, playing an important role in shaping aspen dynamics across the western U.S.

Our in-depth monitoring of seedling survival and growth across two growing seasons in the Brian Head fire in southern Utah revealed the importance of competition in

determining early success following establishment. While seedlings may be outcompeted by suckers where they co-occur, both may represent important parts of a complementary regeneration strategy, where suckers can regenerate existing areas of aspen and seedlings can expand aspen cover into new areas or compensate when sucker regeneration is low. Findings from systematically surveyed fire footprints across the western U.S. support this possibility, as over half of plots containing aspen seedling establishment did not have pre-fire aspen. Our work also adds to our understanding of the impacts of microsite conditions on seedling establishment, with seedlings showing preference for structures such as concavities and coarse woody debris that increase soil moisture, and avoiding areas close to suckers.

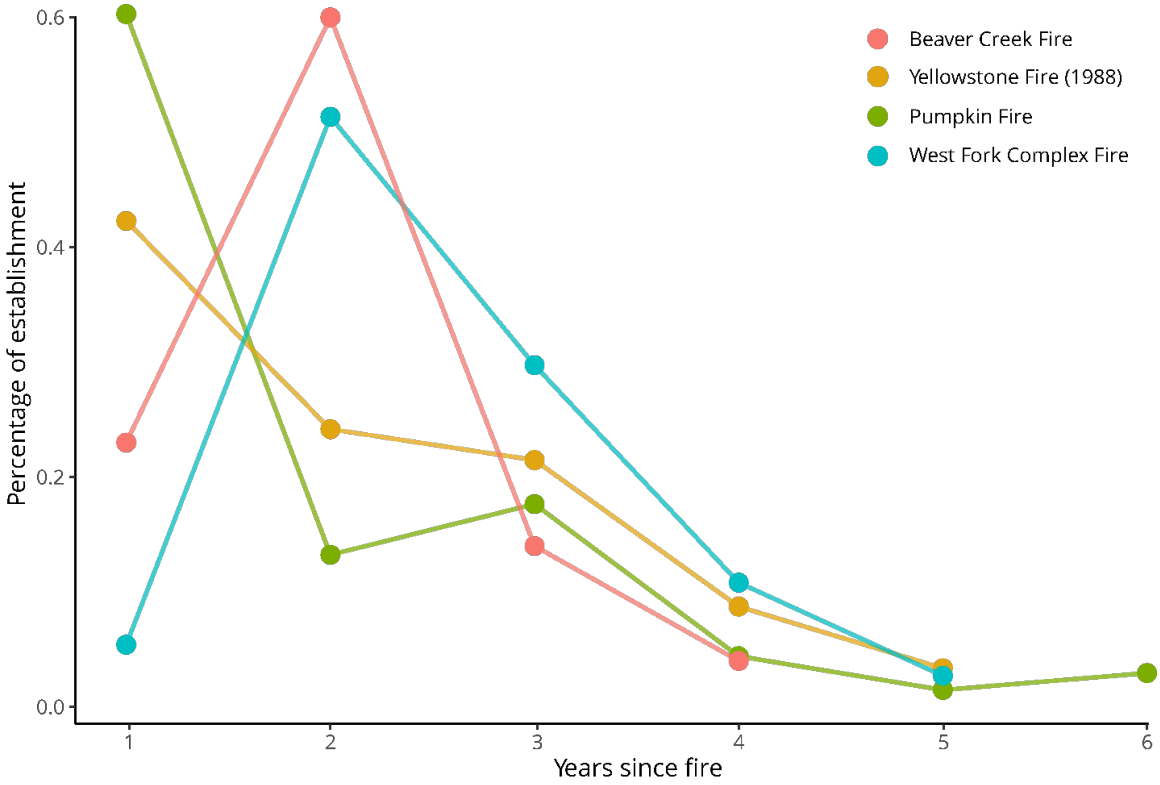
Aspen seedling ecology remains an understudied aspect of aspen ecology. Though many knowledge gaps remain, we highlight the particular importance of *long-term* studies that track survival and growth as well as explore the continued impact of intraspecific competition with suckers and seedlings. It is also important to better understand drivers of aspen seed-availability across time and space, given that this is likely an important factor of why some areas have only low-level seedling establishment while others have high density, widespread establishment.

Overall, we hope that this research encourages managers and researchers to reconsider previously held assumptions about seedling establishment in aspen. Continued increases in our knowledge of sexual regeneration dynamics in aspen are dependent on an increased awareness that seedling establishment is a feasible and likely common part of post-disturbance environments across the west. We encourage managers and researchers to search post-disturbance areas for the presence of seedlings, and subsequently protect

and monitor seedling populations and the genetic and phenotypic diversity they contain. Effective identification of aspen seedlings is the first step toward better understanding how seedlings shape aspen communities, and contribute broadly to post-fire forest regeneration and resilience in the western U.S.

APPENDICES

Appendix A. Seedling Establishment Over Time In Historical Sites



Percent of seedling establishment in each year following the Beaver Creek (1985), Yellowstone (1988), Pumpkin (2000), and West Fork Complex (2013) fires. These were the only studies with multiple years of establishment which reported the relative percentage of seedlings establishing each year. Though Quinn and Wu (2001) did document seedling establishment in multiple years after the Rattlesnake Fire we were not able to determine establishment percentages across years from the published data.

Appendix B. Establishment Climate Model Results

Parameter posterior estimates for establishment climate models. Compatibility intervals of 50% and 89% are shown, as well as the proportion of the posterior that was below or above 0, depending if the mean was negative or positive, respectively (f). Proportion below/above zero is not shown for sigma parameters, since this variance term is by definition above 0. Variables with an asterisk have been inverted (multiplied by -1) so that all precipitation-related variables share a common scale, where positive values represent wetter conditions than average, and negative values represent drier conditions.

Model	Parameter	Mean	5.5%	25%	75%	94.5%	f
Annual precipitation	α	-0.448	-0.707	-0.183	-0.557	-0.339	0.995
	Sigma	0.958	0.780	1.180	0.870	1.031	—
	β Temperature	0.090	-0.210	0.390	-0.034	0.218	0.686
	β Precipitation	-0.170	-0.472	0.126	-0.296	-0.043	0.818
Annual temperature	α	0.548	0.176	0.914	0.393	0.706	0.988
	Sigma	1.376	1.127	1.684	1.249	1.482	—
	β Temperature	0.039	-0.395	0.466	-0.139	0.220	0.563
	β Precipitation	0.530	0.102	0.951	0.350	0.708	0.975
Annual climate water deficit*	α	-0.246	-0.510	0.019	-0.353	-0.135	0.933
	Sigma	0.929	0.753	1.142	0.840	1.005	—
	β Temperature	-0.100	-0.390	0.185	-0.217	0.018	0.716
	β Precipitation	0.100	-0.197	0.394	-0.017	0.219	0.716
Annual vapor pressure deficit*	α	-0.220	-0.638	0.192	-0.395	-0.045	0.803
	Sigma	1.545	1.261	1.897	1.405	1.665	—
	β Temperature	0.062	-0.419	0.547	-0.140	0.263	0.586
	β Precipitation	-0.053	-0.533	0.423	-0.249	0.140	0.575
Annual Palmer Drought Severity Index	α	-0.437	-0.745	-0.132	-0.562	-0.310	0.989
	Sigma	1.125	0.915	1.386	1.019	1.214	—
	β Temperature	-0.181	-0.530	0.165	-0.331	-0.030	0.795
	β Precipitation	0.215	-0.141	0.567	0.070	0.362	0.837
Summer precipitation	α	-0.259	-0.490	-0.027	-0.352	-0.166	0.962
	Sigma	0.836	0.681	1.028	0.758	0.902	—
	β Temperature	0.123	-0.120	0.363	0.022	0.223	0.797
	β Precipitation	-0.150	-0.385	0.085	-0.249	-0.052	0.853
Summer temperature	α	0.446	0.111	0.783	0.305	0.586	0.984
	Sigma	1.226	1.002	1.494	1.114	1.320	—
	β Temperature	-0.140	-0.474	0.206	-0.283	0.001	0.747
	β Precipitation	0.328	-0.007	0.670	0.179	0.472	0.940
Summer climate water deficit*	α	-0.083	-0.307	0.138	-0.177	0.010	0.727
	Sigma	0.814	0.662	0.995	0.737	0.879	—
	β Temperature	-0.254	-0.478	-0.025	-0.349	-0.161	0.959
	β Precipitation	0.215	-0.015	0.447	0.120	0.307	0.933
Summer vapor pressure deficit*	α	-0.082	-0.455	0.284	-0.234	0.071	0.644
	Sigma	1.342	1.092	1.651	1.218	1.445	—
	β Temperature	0.039	-0.340	0.413	-0.115	0.195	0.568
	β Precipitation	0.037	-0.339	0.418	-0.120	0.196	0.562
Summer Palmer Drought Severity Index	α	-0.421	-0.713	-0.131	-0.544	-0.298	0.988
	Sigma	1.077	0.877	1.315	0.977	1.166	—
	β Temperature	-0.360	-0.662	-0.056	-0.484	-0.237	0.970
	β Precipitation	0.194	-0.115	0.504	0.067	0.319	0.848
Average length of wet streaks	α	-0.398	-0.576	-0.221	-0.472	-0.325	1.000
	Sigma	0.625	0.509	0.772	0.567	0.673	—
	β Temperature	-0.016	-0.201	0.170	-0.091	0.060	0.560
	β Precipitation	-0.020	-0.197	0.164	-0.096	0.055	0.572

Number of days with precipitation	α	-0.228	-0.421	-0.033	-0.309	-0.148	0.966
	Sigma	0.676	0.545	0.839	0.610	0.731	—
	β Temperature	0.086	-0.110	0.288	0.002	0.170	0.757
	β Precipitation	-0.069	-0.261	0.122	-0.150	0.011	0.720
Rain intensity	α	-0.197	-0.447	0.052	-0.298	-0.096	0.895
	Sigma	0.899	0.730	1.109	0.814	0.970	—
	β Temperature	0.215	-0.049	0.471	0.109	0.323	0.907
	β Precipitation	0.041	-0.220	0.301	-0.069	0.152	0.597

Appendix C. Model Results For Brian Head Occupancy, Microsite Preference, Abundance, Survival And Growth Models

Parameter posterior estimates for aspen seedling plot occupancy model. Compatibility intervals of 50% and 89% are shown, as well as the proportion of the posterior that was below or above 0, depending if the mean was negative or positive, respectively (f).

Parameter	Mean	5.5%	25%	75%	94.5%	f
α	0.674	0.169	0.457	0.888	1.192	0.986
β Elevation	1.577	0.848	1.249	1.889	2.349	1.000
β dNBR	-0.238	-0.826	-0.473	0.003	0.325	0.747
β Aspect	0.491	-0.112	0.224	0.741	1.123	0.902
β Herbaceous vegetation	0.147	-0.404	-0.092	0.381	0.708	0.656
β Sucker density	-0.064	-0.589	-0.284	0.154	0.466	0.577
β Slope	-0.112	-0.656	-0.343	0.122	0.428	0.627
β Seed source distance	-0.980	-1.657	-1.238	-0.704	-0.358	0.996

Parameter posterior estimates for aspen sucker plot occupancy model. Compatibility intervals of 50% and 89% are shown, as well as the proportion of the posterior that was below or above 0, depending if the mean was negative or positive, respectively (f).

Parameter	Mean	5.5%	25%	75%	94.5%	f
α	2.101	1.346	1.747	2.414	2.964	1.000
β Elevation	2.249	1.351	1.839	2.629	3.250	1.000
β dNBR	-0.635	-1.344	-0.916	-0.337	0.031	0.937
β Aspect	-0.151	-0.889	-0.459	0.162	0.581	0.625
β Herbaceous vegetation	-0.314	-0.965	-0.578	-0.043	0.311	0.783
β Slope	0.338	-0.286	0.065	0.600	1.000	0.800
β Seed source distance	-0.849	-1.507	-1.102	-0.577	-0.241	0.989

Parameter posterior estimates for aspen seedling plot abundance model. Compatibility intervals of 50% and 89% are shown, as well as the proportion of the posterior that was below or above 0, depending if the mean was negative or positive, respectively (f).

Parameter	Mean	5.5%	25%	75%	94.5%	f
α	7.624	7.016	7.374	7.874	8.225	1.000
Sigma	2.542	2.113	2.334	2.722	3.055	1.000
β Elevation	0.609	-0.114	0.313	0.910	1.330	0.912
β dNBR	0.103	-0.627	-0.199	0.401	0.819	0.595
β Aspect	0.501	-0.180	0.212	0.790	1.184	0.881
β Herbaceous vegetation	-0.519	-1.210	-0.806	-0.231	0.168	0.888
β Sucker density	-0.524	-1.170	-0.790	-0.256	0.114	0.905
β Slope	-0.156	-0.779	-0.413	0.106	0.466	0.659
β Seed source distance	-1.296	-1.982	-1.579	-1.011	-0.614	0.998

Parameter posterior estimates for microsite preference models. Compatibility intervals of 50% and 89% are shown, as well as the proportion of the posterior that was below or above 0, depending if the mean was negative or positive, respectively (f). Proportion below/above zero is not shown for available and observed microsite percentages, since these values are by definition between 0 and 1.

Parameter	Category	Type	Mean	5.5%	25%	75%	94.5%	f
Topo 2.5	Flat	*Available*	0.366	0.344	0.356	0.375	0.388	—
	Concave		0.068	0.057	0.063	0.073	0.080	—
	Sloping		0.566	0.543	0.557	0.576	0.589	—
	Flat	*Observed*	0.373	0.350	0.363	0.383	0.396	—
	Concave		0.126	0.111	0.119	0.133	0.143	—
	Sloping		0.501	0.477	0.491	0.511	0.524	—
	Flat	*Preference*	0.022	-0.064	-0.016	0.058	0.111	0.652
	Concave		0.871	0.503	0.699	1.022	1.297	1.000
	Sloping		-0.115	-0.170	-0.138	-0.092	-0.059	1.000
Topo 50	Flat	*Available*	0.119	0.104	0.112	0.125	0.134	—
	Concave		0.017	0.012	0.014	0.019	0.023	—
	Sloping		0.864	0.848	0.858	0.871	0.879	—
	Flat	*Observed*	0.086	0.074	0.080	0.092	0.100	—
	Concave		0.045	0.036	0.041	0.049	0.056	—
	Sloping		0.868	0.852	0.862	0.875	0.884	—
	Flat	*Preference*	-0.270	-0.408	-0.335	-0.213	-0.113	0.995
	Concave		1.829	0.806	1.291	2.263	3.129	1.000
	Sloping		0.005	-0.021	-0.006	0.016	0.031	0.614
Sucker distance	0–50	*Available*	0.091	0.079	0.086	0.097	0.104	—
	15–50		0.254	0.234	0.245	0.262	0.274	—
	50–100		0.191	0.174	0.183	0.198	0.209	—
	100–200		0.107	0.094	0.101	0.113	0.121	—
	200+		0.357	0.336	0.348	0.366	0.378	—
	0–50	*Observed*	0.022	0.016	0.019	0.025	0.030	—
	15–50		0.267	0.246	0.258	0.276	0.288	—
	50–100		0.223	0.204	0.215	0.231	0.243	—
	100–200		0.151	0.135	0.144	0.159	0.169	—
	200+		0.336	0.313	0.326	0.346	0.359	—
	0–50	*Preference*	-0.753	-0.831	-0.792	-0.720	-0.658	1.000
	15–50		0.056	-0.059	0.005	0.104	0.178	0.772
	50–100		0.172	0.027	0.108	0.232	0.328	0.973
	100–200		0.421	0.192	0.315	0.519	0.674	0.999
	200+		-0.057	-0.140	-0.094	-0.022	0.029	0.856
Small CWD	Presence	*Available*	0.107	0.097	0.103	0.112	0.118	—
	Absence		0.893	0.882	0.888	0.897	0.903	—
	Presence	*Observed*	0.206	0.187	0.198	0.214	0.226	—
	Absence		0.794	0.774	0.786	0.802	0.813	—
	Presence	*Preference*	0.931	0.682	0.819	1.036	1.205	1.000
	Absence		-0.111	-0.135	-0.121	-0.101	-0.087	1.000
Large CWD	Presence	*Available*	0.086	0.077	0.082	0.090	0.096	—
	Absence		0.914	0.904	0.910	0.918	0.923	—
	Presence	*Observed*	0.115	0.100	0.109	0.122	0.131	—
	Absence		0.885	0.869	0.878	0.891	0.900	—
	Presence	*Preference*	0.342	0.119	0.240	0.436	0.585	0.996
	Absence		-0.032	-0.051	-0.040	-0.023	-0.012	0.996

Parameter and categorical contrast posterior estimates for aspen seedling survival model. Compatibility intervals of 50% and 89% are shown, as well as the proportion of the posterior that was below or above 0, depending if the mean was negative or positive, respectively (f). Contrasts are shown for each two-way combination between a predictor's categories. For categorical with two variables, the contrast is for presence of the variable (e.g., the change in survival if the seedling is next to a small CWD; or in a cluster, etc.). For categorical variables with more than two categories, a given contrast, "X:Y", is the difference of X relative to Y. The following codes have been used for sucker distance (1 = 0–15 cm, 2 = 15–50 cm, 3 = 50–100 cm, 4 = 100–200 cm, and 5 = 200+ cm) and large and small topography (1 = flat, 2 = concave, 3 = sloping).

Parameter	Mean	5.5%	25%	75%	94.5%	f
β Elevation	-0.058	-0.220	-0.125	0.010	0.104	0.716
β dNBR	0.088	-0.039	0.034	0.141	0.214	0.869
β Sucker density	-0.343	-0.524	-0.419	-0.268	-0.167	1.000
β Aspect	0.030	-0.103	-0.026	0.086	0.165	0.641
β Seedling density	-0.184	-0.307	-0.236	-0.131	-0.062	0.991
β Slope	-0.002	-0.126	-0.053	0.049	0.122	0.512
β Herbaceous vegetation	0.067	-0.075	0.006	0.127	0.212	0.772
Sucker distance 1:2	-0.182	-1.047	-0.524	0.177	0.644	0.630
Sucker distance 1:3	-0.385	-1.258	-0.733	-0.020	0.446	0.762
Sucker distance 1:4	-0.577	-1.479	-0.934	-0.201	0.277	0.856
Sucker distance 1:5	-0.843	-1.737	-1.195	-0.478	-0.006	0.947
Sucker distance 2:3	-0.203	-0.567	-0.352	-0.054	0.154	0.820
Sucker distance 2:4	-0.395	-0.814	-0.572	-0.217	0.018	0.936
Sucker distance 2:5	-0.661	-1.058	-0.823	-0.498	-0.269	0.997
Sucker distance 3:4	-0.192	-0.593	-0.360	-0.022	0.206	0.778
Sucker distance 3:5	-0.458	-0.842	-0.619	-0.297	-0.073	0.970
Sucker distance 4:5	-0.266	-0.647	-0.426	-0.104	0.114	0.870
Small CWD	0.115	-0.176	-0.006	0.239	0.410	0.738
Large CWD	-0.278	-0.668	-0.440	-0.115	0.104	0.873
Large topo 1:2	0.758	-0.076	0.408	1.101	1.605	0.928
Large topo 1:3	-0.254	-0.803	-0.483	-0.024	0.292	0.770
Large topo 2:3	-1.012	-1.684	-1.286	-0.726	-0.365	0.995
Small topo 1:2	0.050	-0.353	-0.119	0.221	0.455	0.576
Small topo 1:3	-0.234	-0.486	-0.339	-0.127	0.019	0.932
Small topo 2:3	-0.284	-0.679	-0.453	-0.117	0.111	0.874
Cluster	-0.537	-0.786	-0.641	-0.432	-0.286	1.000

Parameter and categorical contrast posterior estimates for aspen seedling growth model. Compatibility intervals of 50% and 89% are shown, as well as the proportion of the posterior that was below or above 0, depending if the mean was negative or positive, respectively (f). Contrasts are shown for each two-way combination between a predictor's categories. For categorical with two variables, the contrast is for presence of the variable (e.g., the change in growth if the seedling is next to a small CWD; or in a cluster, etc.). For categorical variables with more than two categories, a given contrast, "X:Y", is the difference of X relative to Y. The following codes have been used for sucker distance (1 = 0–15 cm, 2 = 15–50 cm, 3 = 50–100 cm, 4 = 100–200 cm, and 5 = 200+ cm) and large and small topography (1 = flat, 2 = concave, 3 = sloping)

Parameter	Mean	5.5%	25%	75%	94.5%	f
Sigma	14.803	13.748	14.335	15.246	15.922	1.000
β Initial height	0.802	-0.697	0.184	1.428	2.280	0.807
β Elevation	-0.039	-2.497	-1.085	0.996	2.492	0.518
β dNBR	0.788	-0.810	0.101	1.467	2.399	0.782
β Seedling density	0.626	-0.880	0.002	1.251	2.121	0.750
β Slope	0.978	-0.661	0.286	1.676	2.607	0.829
β Sucker density	-4.490	-7.026	-5.543	-3.443	-1.952	0.998
β Aspect	-2.546	-4.469	-3.361	-1.745	-0.617	0.981
β Herbaceous vegetation	0.546	-1.417	-0.276	1.381	2.504	0.672
Sucker distance 1:2	-1.719	-11.813	-5.974	2.529	8.274	0.603
Sucker distance 1:3	-7.888	-18.097	-12.083	-3.580	2.066	0.894
Sucker distance 1:4	-4.897	-15.011	-9.186	-0.677	5.042	0.782
Sucker distance 2:3	-6.169	-11.829	-8.554	-3.792	-0.512	0.959
Sucker distance 1:5	1.402	-8.132	-2.693	5.524	10.987	0.592
Sucker distance 2:4	-3.178	-9.250	-5.744	-0.616	2.897	0.798
Sucker distance 2:5	3.121	-2.221	0.853	5.438	8.374	0.824
Sucker distance 3:4	2.991	-2.770	0.552	5.422	8.791	0.796
Sucker distance 3:5	9.290	4.218	7.184	11.442	14.283	0.999
Sucker distance 4:5	6.299	1.574	4.350	8.293	10.960	0.986
Small CWD	1.465	-2.831	-0.345	3.257	5.748	0.710
Large CWD	-0.749	-6.361	-3.095	1.635	4.883	0.587
Large topo 1:2	-0.707	-10.251	-4.911	3.438	8.954	0.546
Large topo 1:3	2.461	-4.008	-0.205	5.169	8.846	0.733
Large topo 2:3	3.168	-5.153	-0.340	6.722	11.463	0.726
Small topo 1:2	0.416	-4.965	-1.788	2.691	5.760	0.546
Small topo 1:3	2.665	-0.799	1.208	4.136	6.106	0.891
Small topo 2:3	2.249	-3.058	-0.022	4.464	7.650	0.748
Cluster	-2.933	-6.627	-4.481	-1.350	0.768	0.898